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The Metalimnetic Oxygen Maximum in Myers Lake¹

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ABSTRACT

In 1951 (and for four successive summers thereafter) Myers Lake in Marshall County in northern Indiana developed a pronounced and very persistent oxygen maximum at about 8 meters, well down in the metalimnion. Oxygen concentrations at this level ranged as high as 23.3 ppm, with mean summer values of 18.35, 19.98, 13.98, and 15.71 ppm for the summers of 1952-1955, respectively.

The oxygen maximum is correlated chiefly with a dense population of *Oscillatoria agardhii*, which is the dominant phytoplankton the year round in Myers Lake. Other alga species include *Aphanizomenon flos-aquae* and *Melosira* sp. in the upper metalimnion, and *Gomphosphaeria*, *Anacystis*, and *Anabaena* in the epilimnion. Myers Lake can be characterized as a "bluegreen-diatom" lake.

Oxygen production was measured using the light-dark bottle method. Daily gross production rates as high as 1377 $\mu\text{g O}_2/\text{L}$ were found in the metalimnion with a mean value at 8 m of 754 $\mu\text{g O}_2/\text{L}$. Mean gross production in the metalimnion was more than 50% greater than mean rates for the epilimnion, while net production at 7 and 8 m was more than four times higher than the highest epilimnetic rates. Total gross production in the West Basin averaged 3.94 g O_2 (1.48 g C)/ m^2/day .

Average light intensity at the level of the oxygen maximum was about one to two per cent of surface illumination ($k_{1\%} = 0.54$), but the photosynthesis tests showed some assimilation taking place at less than 0.5% illumination. *Oscillatoria agardhii* produced a dense growth at 8-10 m with light intensities estimated at from 200 - 500 lux and temperatures of about 7-9°C.

The small daily net production of oxygen in the metalimnion can accumulate to form the large maxima observed in the lake only if the metalimnion is protected from turbulent disturbances. The extent of eddy diffusion can be estimated from temperature changes that occur in the clinolimnion. Mean values of the clinolimnetic coefficient of eddy conductivity varied from 0.09 to 0.50, being inversely correlated with the mean summer oxygen maxima.

Overall stability of a lake is affected by the shape of the lake basin, climatic conditions early in the spring, degree of protection afforded by the lake's surroundings, etc. Myers Lake has very steep sides (volume development = 1.17 for the West Basin). Because it is surrounded by a high bank covered by a dense growth of trees, the thermocline forms early in the season at a relatively shallow level (above three meters). As stratification proceeds, the intensity of the thermal gradient increases, making it more difficult for wind-induced turbulence to penetrate the metalimnion. Mean stability of Myers Lake ranged from 466 to 507 g/ cm^2 , with a positive correlation between stability and mean summer oxygen maxima.

Myers Lake is compared with some other lakes showing similar oxygen maxima, and a brief contribution toward a generalized theory of the metalimnetic oxygen maximum is presented.

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INTRODUCTION

A lake is in a sense an isolated, autonomous unit. The activities of the diverse biota living within its confines serve to give the lake itself certain characteristics analogous to a living organism. Thus it is customary to speak of the complex internal chemical exchanges as the metabolism of the lake. As in its biological counterpart, the metabolism of a lake is seen to consist of two phases—anabolism and catabolism. Anabolic activities are concerned with the fixing of simple inorganic nutrients into organic form, in short, photosynthesis. Catabolism is the oxidation of these organic substances to release energy for biological activity and to furnish material for new organic compounds. This is respiration.

Oxygen is produced as a result of anabolic processes and is consumed by catabolic activities. Measurement of the dissolved oxygen can give valuable clues to the metabolic balance of the lake. The amount of oxygen present at any given time represents the net balance of production over consumption (except for such amounts of atmospheric oxygen that may have got into the surface strata by diffusion or agitation). An oxygen curve (oxygen "profile") constructed by plotting the concentrations of oxygen present at various depths in the lake is perhaps the most valuable single diagnostic character revealing the nature of the lake.

In the summer of 1951 Myers Lake in Northern Indiana was found to have a pronounced oxygen maximum at 8-9 meters, well down in the metalimnion. This condition, which persisted throughout the summer, has been observed during five successive summers. It seems to be characteristic of Myers Lake. Since that time several more lakes have been found to show similar patterns of oxygen distribution. Frey (1955), in summarizing the oxygen data for 90 lakes of Northern Indiana up to 1954, reported that 26 showed such a plus-heterograde (a term introduced by Åberg and Rodhe 1942) type of oxygen profile for one or more years.

The plus-heterograde type of oxygen distribution may involve concentrations of oxygen in excess of saturation values. A supersaturation of oxygen may be due to physical or biological causes. Physical supersaturation, which results from the warming of oxygen-saturated water without the loss of any of the dissolved oxygen, is usually not of so great a value nor is it so long lasting as biologically produced supersaturation. Perhaps many cases of low oxygen supersaturation observed early in the summer in which the concentration of oxygen does not exceed the saturation value at the minimum winter temperature of that stratum are produced physically.

A biological supersaturation results from an accumulation of oxygen produced by photosynthesis. This occurs quite commonly in the epilimnion if the water is calm and a large population of plants is present. Woodbury (1941) observed oxygen concentrations in Lake Waubesa, Wisconsin, as high as 32.1 ppm at the surface and 16.8 ppm at a depth of 12 feet produced by a dense bloom of *Chlamydomonas*. Excess oxygen in the epilimnion rarely exceeds the amount which the chlorophyll-bearing organisms can produce in a single day, because under even ordinary con-

ditions of wind disturbance this excess oxygen is dissipated rapidly, rarely lasting overnight (see Birge and Juday 1911).

A photosynthetic oxygen maximum occurring in the metalimnion is of considerably more interest. It is by far the least common of the various types of oxygen supersaturation. Furthermore, it may (and usually does) persist throughout the entire period of stratification and often produces oxygen concentrations in excess of 200% saturation. The highest concentration observed in Myers Lake was 23.3 ppm, which was 224% saturation.

This amount of oxygen is sufficient to be of significance in the bioeconomy of the lake. A stratum of high oxygen concentration might act as a barrier interrupting the vertical distribution of a species. The reaction of animal species to high oxygen tension varies considerably. Frey (1955) suggested that the cisco may avoid the stratum with the highest oxygen concentration. Woodbury (1941) described a case of gas embolism in the capillaries of fish killed by exposure to high oxygen concentrations. Wiebe (1931) and Bean and Rottschäfer (1938) also reported undesirable effects of high oxygen tension to fish. The presence of a metalimnetic oxygen maximum can make the deeper waters of a lake habitable to certain cold stenothermal species with high oxygen requirements that otherwise would not be able to live there. Such species include cisco and trout, both of which have survived not only in oligotrophic lakes with orthograde oxygen curves but in many smaller eutrophic lakes with a plus-heterograde oxygen distribution. Frey (1955) believes that the presence of an oxygen maximum in the metalimnion is the dominant factor responsible for the survival of cisco in Indiana lakes smaller than 60 ha in size.

From the standpoint of fish ecology as well as increasing our knowledge of basic limnological phenomena, it seems desirable to have as complete an understanding as possible of the factors that lead to the formation and maintenance of a high oxygen level in the metalimnion. For this reason the writer has investigated the general limnology of Myers Lake and has attempted to relate it where possible to the metalimnetic oxygen maximum. It is also possible, by making comparisons with other lakes showing similar maxima, to make a contribution toward a generalized theory of the metalimnetic oxygen maximum.

It has been necessary to adopt certain qualifications in the use of the term metalimnetic oxygen maximum. The plus-heterograde oxygen curve of Åberg and Rodhe applies to any pattern of oxygen distribution where the largest amount of dissolved oxygen exists at some level below the surface. This maximum may or may not be in the metalimnion, may be persistent or may exist only during the day if the weather is calm, and may bear any relation to the saturation concentration of the stratum in which it is located. A metalimnetic oxygen maximum as used by the writer refers to a maximum concentration of biologically produced oxygen in the metalimnion which persists for some time (several weeks to 3 or 4 months) and which normally exceeds the prestratification saturation value.

Metalimnetic oxygen maxima have been reported several times in the literature, but nothing beyond certain generalizations has ever been pro-

posed concerning the factors producing such a maximum. Birge and Juday (1911) reported oxygen maxima of 36.5 ppm in Knights Lake at a depth of 4.5 m on August 26, 1909, and 35.7 ppm (also at 4.5 m) in Otter Lake on July 25, 1910. Other lakes in the same chain in southeastern Wisconsin that showed oxygen maxima in the metalimnia were Beasley, Long, and Rainbow. Birge and Juday attributed the production of this oxygen maximum to the stability of the metalimnion and to high transparency which permits algae in this zone to carry on photosynthesis. They also mentioned that the depth of maximum oxygen concentration does not always correspond with the depth of maximum phytoplankton population, but they do not give an explanation.

Scott (1916) observed epilimnial oxygen supersaturations up to 120.2% in several Indiana lakes, but found no cases of metalimnetic maxima. He suggested that a sub-surface maximum could result from a decrease of oxygen in the surface strata due to the decay of plankton organisms as well as from the actual production of oxygen by the algae in the lower layers. He described the occasional abundance of disintegrating *Microcystis* colonies found near the surface of several of the lakes he examined. In the graphs and tables given in the appendix of Scott's paper, the difference between the oxygen concentrations at the surface and the sub-surface maxima (usually at 2-4 m) rarely exceeded 2 or 3 ppm, and the maxima never exceeded 100% saturation at the temperature given for that stratum. It should be pointed out that both the sub-surface photosynthetic production of oxygen and the catabolic reduction of the surface oxygen (even though they occur in the epilimnion) will produce the plus-heterograde oxygen curve of Åberg and Rodhe.

After study of more Indiana lakes, Scott (1931) reported several cases of true metalimnetic oxygen maxima. He found a saturation of 158% (16.0 ppm) in Lake Gage at 8 m on July 6, 1929, which was correlated with a bloom of *Lyngbya* in the 5-10 m level. On August 3 there was still a saturation of 153% even though the amount of phytoplankton had declined. The 8 m stratum of Clear Lake had an oxygen saturation of 139% on July 15 and 134% on August 5 of the same year. Scott agreed with Birge and Juday that a supersaturation in the metalimnion is much more permanent than one developed in the epilimnion because the water of the metalimnion is not exposed to the air. Scott observed that the supersaturation may persist for a considerable period after the decline of the plankton flora that produced it (in other words, loss of oxygen through respiration, diffusion, and decay is very slow), and also that such a condition is very persistent, usually lasting until the sinking of the thermocline restores the circulation of the water with that of the epilimnion. Usually this does not occur in deep water maxima until the fall overturn, but exceptionally shallow maxima may be destroyed by a sinking thermocline during the summer (see data on Wyland Lake, p. 36).

Thienemann (1928) reported only one example that approaches the concept of a true metalimnetic oxygen maximum. This was in Garrensee, which he characterized as a "*Lobelia-Isoetes* lake." On August 17, 1917, Garrensee had an oxygen concentration of 8.75 cc/L (117.5% saturation) at 8 meters. This is still slightly under the saturation value at 4°, so that it is uncertain from a single sample whether this is photosynthetically produced oxygen or residual oxygen from the time of vernal circulation.

Since the transparency was 6.5 m it is very possible that assimilation took place at 8 m. Some other lakes in Germany were noted to develop small metalimnetic oxygen maxima early in the spring, which later changed to oxygen minima in the summer. These maxima were largely due to supersaturation produced by physical means and were below the compensation level of the phytoplankton. Thienemann related the excess of oxygen in Garrensee to increased eutrophication of the lake. He suggested the possibility of oxygen production in the deeper waters, but at that time no proof was offered of the relationship between the metalimnetic oxygen content and assimilation of the phytoplankton.

Yoshimura (1938), in describing the oxygen distribution in more than 200 lakes of Japan, made special note of 18 mesotrophic and eutrophic lakes with metalimnetic oxygen maxima ranging up to 15.65 cc/L (258%). In all but two of these latter lakes the oxygen maxima were due to assimilation by phytoplankton. Yoshimura mentioned blue-green algae as the cause in 8 cases and diatoms in 6. He noted also that the maximum phytoplankton density does not always occur at the same depth as the maximum concentration of oxygen. He felt that the epilimnion would have a much higher oxygen content if it were not for the reduced hydrostatic pressure there and the nocturnal cooling and turbulent motion bringing that water into contact with surface water of lower oxygen content. The lakes of Japan with high oxygen content in the metalimnion were all small, well-protected mountain lakes with high transparency. Yoshimura also noted the influence of climatic conditions, since the highest oxygen values were observed in the summer of 1933, the warmest and calmest summer for the past ten years. He concluded that in order for a lake to show a metalimnetic oxygen maximum, the compensation level (1.2 times the transparency in Japanese lakes) must fall below the upper level of the metalimnion.

Welch (1952) mentioned that in the lakes of Michigan no excesses of dissolved oxygen greater than 195% have been found, without stating whether these maxima were found in the epilimnion or in the metalimnion. Ruttner (1953) related the metalimnetic oxygen maximum to the stable stratification existing in the metalimnion and the great reduction there of eddy diffusion.

There are essentially two aspects to the investigation of the metalimnetic oxygen maximum. The first is the actual production of the oxygen. This may be called the ecological phase and involves basically a study of the organism(s) producing the oxygen and all the environmental influences, both biotic and physical, affecting the photosynthesizing organisms. The second deals with the retention and accumulation of the oxygen. The factors involved here are chiefly physical (except respiration and decay which contribute toward the reduction of the oxygen) and concern mainly the stability of the water mass of the metalimnion. This stability is a product of the morphometry of the lake basin, the geomorphic setting of the lake, intensity of thermal stratification, gross effect of the wind, and other climatic factors. It will be noted that these are the same two elements suggested by Birge and Juday in 1911.

METHODS

Chemical methods

Water samples for chemical analysis were collected either by means of a Kemmerer sampler or a British type aluminum water sampler of 1-liter capacity. Samples for oxygen analysis were placed in 300-ml B.O.D. bottles, while samples for other purposes were usually placed in standard magnesium citrate bottles.

Oxygen was usually determined by the unmodified Winkler method, described in any water chemistry manual (*e.g.*, Welch 1948, Ellis *et al.* 1948, Standard Methods 1955). Often some modification of the Winkler must be used to compensate for interferences of various sorts. On several occasions the water when tested for the presence of interfering substances according to procedures in Ellis *et al.* (1948, p. 16) consistently gave negative results. The sample-blank method (Ellis *et al.*, p. 13) was also used several times and indicated no interfering substances in quantity sufficient to disturb the results.

For the determination of chlorophyll a 500-ml sample was filtered through a membrane filter (millipore filter, type HA) after which the membrane was allowed to dry in an oven at about 60° C for an hour. The membrane was next flooded with absolute methyl alcohol in a petri dish and left overnight. The material was then filtered through an ordinary paper filter to remove fragments of the membrane filter. The filtrate was diluted to 25 ml in a volumetric flask, and the optical density measured with a Klett-Summerson colorimeter using a red filter (about 640 m μ). Amounts of chlorophyll were calculated from a standardization curve constructed from various dilutions of a standardized solution of pure chlorophyll *a* secured from Nutritional Biochemicals Corporation.

The rate of photosynthesis was determined by the standard light and dark bottle method (see Ryther 1956b for a recent evaluation of this technique). A series of glass-stoppered bottles varying in capacity from 100 to 110 ml was painted black and covered with masking tape to prevent the paint from being scratched off. There was a matching series of clear glass bottles. The bottles, filled with water from the depth at which they were to be suspended, were placed in wire baskets tied to a cable at various depths (usually 0, 4, 6, 8, 10, and 12 m) and hung from a cross bar fastened between 2 small barrels. The cable, which was only slightly longer than the depth of the water, was anchored to the bottom. Samples were titrated by the unmodified Winkler method, and the results were corrected for volume of reagents.

Methyl orange alkalinity is reported as ppm of CaCO₃ (Standard Methods 1955). Calcium was determined by the versenate titration method of Heron and Mackereth (1955). The pH was determined by a Beckman model G pH meter. Specific conductance was measured by a Wheatstone Bridge apparatus. The specific conductance is the reciprocal of the resistance in mho $\times 10^{-6}$ at 18° C.

Soluble phosphorus was determined colorimetrically by taking 50 ml of water that had been filtered through the millipore filter and adding 1 ml of 10% acidified ammonium molybdate solution and 2 drops of stannous chloride (Ellis *et al.*, p. 18). After exactly eight minutes the color was read in the colorimeter using a red filter (640 m μ). A calibra-

tion curve was prepared from various dilutions of standard monobasic potassium phosphate.

Plankton methods

The dominant phytoplankter of the metalimnion is *Oscillatoria agardhii*. It was discovered early that as much as 75% of these filaments was being lost through the pores of the net on the plankton trap even though it was no. 20 mesh. Thereafter, all phytoplankton counts were made on whole water samples. To 97 ml of water was added 3 ml of commercial formalin. In counting, 3 aliquots from each sample were examined in a standard Sedgwick-Rafter cell. A total of 25 fields (each 1 mm² in area) was counted in each aliquot at a magnification of 100x, and the average of the 3 aliquots used for the sample. Filaments were measured according to the second method of Olson (1950) which gives lengths in terms of units of 0.1 mm. Olson provided a correction factor of 1.11, which compensates for varying angles of the filaments within the counting grid. Volumes were calculated using an average diameter of 5 microns. The volume of one unit is 1963.5 μ^3 . Volumes for other forms were calculated separately.

For determining the number (C) of filaments or cells (*i.e.*, unicellular forms) per liter, the number in 25 fields (N) is multiplied by a correction factor for the dilution of the water by the preservative (100/97) times a factor converting 25 mm³ to a liter (40,000). The equation is

$$C = N \times 100/97 \times 40,000 \quad (1)$$

In practice, the logarithm of the constant factors was added to the log of N .

$$\log C = \log N + 4.61529 \quad (2)$$

Three additional factors are involved in determining the volume (V) of phytoplankton. For filamentous forms, one must take into account the total length of filaments in 25 fields given in units of 0.1 mm (M), the volume of each unit, and the correction factor (1.11). This equation is

$$V = M \times 100/97 \times 40,000 \times 1.11 \times 1963.5 \quad (3)$$

Again combining the constants in this equation and converting to logarithms we have

$$\log V = \log M + 7.95364 \quad (4)$$

The result (V) is expressed as μ^3 /liter. Volume of non-filamentous forms is determined by using the number of cells per liter (as in equation 1 or 2) and multiplying by the average volume of each cell, omitting the 1.11 correction factor.

Physical methods

Temperature was taken by four different thermometers during the course of this investigation. These included a regular reversing thermometer, two models of a Mortimer-type thermistor thermometer, and a Whitney-type thermistor unit. All were standardized. Even though the thermistors are capable of giving results to hundredths of a degree, for general limnological purposes readings to the nearest tenth of a degree are sufficient.

Transparency was measured by a 20-cm Secchi disc. Light penetra-

tion was measured by a Whitney underwater photometer. Values are expressed as per cent of surface light present in lower strata.

MYERS LAKE

Location and geology

Myers Lake (also called Meyers or East Lake) is a part of Twin Lakes, about 4 miles southwest of Plymouth, Indiana, in Marshall County. It is located in the northeast quarter of Sec. 24, T.33 N., R.1 E. (West Township) and the northwest quarter of Sec. 19, T.33 N., R.2 E. (Center Township). Twin Lakes, instead of being just two lakes, is in reality a closely associated group of six (Fig. 1). Four of these are in direct

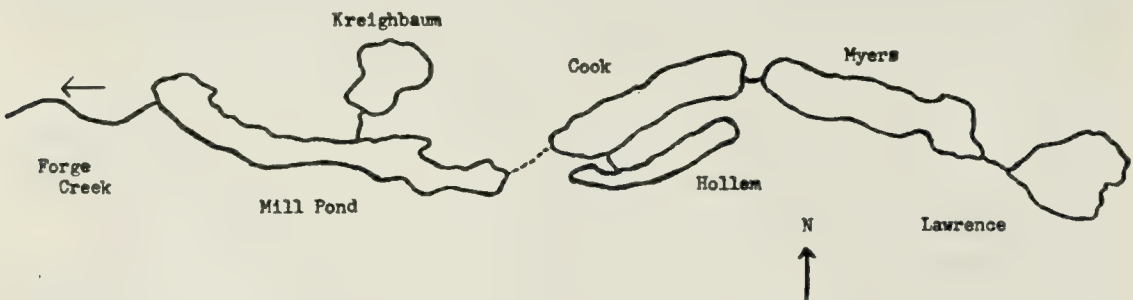


FIG. 1. Twin Lakes chain, Marshall County.

linear sequence: Lawrence, Myers, Cook, and Mill Pond. Hollem adjoins Cook on the south, and Kreighbaum connects with Mill Pond on the north.

Myers Lake lies in the physiographic region of Indiana known as the Steuben Morainial Lake Section of the Northern Moraine and Lake Region (Mallott 1922). Geologically it is located in the Maxinkuckee moraine which formed the western boundary of the Saginaw lobe of the late Wisconsin period. The Maxinkuckee moraine is a lateral moraine extending northward from the Wabash River some 10 miles west of Logansport to the state line north of South Bend.

The entire county is covered to a depth of more than 200 feet with glacial drift. No bedrock is exposed anywhere in the county. Drainage of Myers Lake is mostly internal, the only surface inlet being the small outlet channel from Lawrence Lake. The immediate watershed area of Myers Lake is very small: the land slopes away from the lake from the top of the ridge closely surrounding the lake. Most of the dissolved inorganic material must be leached from the surrounding drift, and since most of the drainage is away from the lake, there are less dissolved nutrients seeping into the lake than if it were the center of a large drainage area.

The origin of the Twin Lakes chain is uncertain. Scovell (in Blatchley and Ashley 1901) suggested that Hollem, Myers, and Lawrence (Lorance) lakes occupy part of an old drainage channel. Cook rather than Hollem should be considered in the direct line with the other two. Because of the irregularities of the bottoms of the lakes and the separation into definite basins (there are 2 in Myers Lake) it seems more likely that the lakes are of ice block origin. Dr. William J. Wayne (personal communication) suggested that the lakes may have been formed by an "ice-cored moraine" (a term introduced by Goldthwait 1951) that was buried by a readvance of the ice, covered with till, then melted in several hun-

dred years. The major blocks of ice formed the basins of Lawrence Myers, Hollem, Cook, and Kreighbaum lakes. A common outlet developed at least for Lawrence, Myers, and Cook lakes, leaving the other two with chiefly sub-surface drainage.

The deepening of the outlet (Forge Creek) gradually lowered the level of the 3 main lakes. In 1836 a dam was placed in Forge Creek about $1\frac{1}{2}$ miles downstream from Cook Lake to provide power for a grist mill. This dam, which provided a head of about 15 feet, has been rebuilt and is maintained by the United States Geological Survey. The installation of this dam flooded the creek back of the dam to a depth of about 15 feet, creating Mill Pond Lake, raised the level of Cook, Myers, and Lawrence lakes somewhat, and connected Hollem with Cook and Kreighbaum with Mill Pond. Most of the areas between Lawrence and Myers lakes and Cook and Myers have been filled in to provide roadways and one railroad bed.

Morphometry

The contour map of Myers Lake (Fig. 2) was prepared by the Indiana Department of Conservation in 1954 with the aid of an echo sounder.

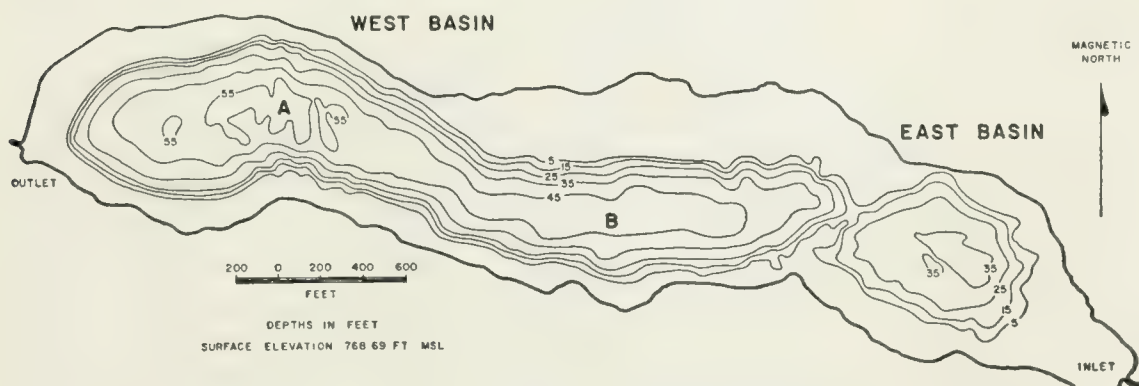


FIG. 2. Hydrographic map of Myers Lake, showing location of sampling stations. (Adapted from map prepared by the U. S. Geological Survey and the Indiana Department of Conservation.)

Calculations from planimeter measurements made directly from this map were used to construct hypsographic curves from which the data in Table 1 were obtained. The various morphometric parameters of the table are after Welch (1948).

Myers Lake lies in an elongate depression about 50 feet below the level of the surrounding land. The bank at the west end, which is largely man-made, supports the railroad and a public roadway, while the one at the east end between Myers Lake and Lawrence Lake, mostly filled in and also supporting a public road, is the lowest. The lake itself largely fills the depression, leaving very little beach. The lake proper is an elongate, slightly sinuous expanse of water about 1675 m maximum length and varying in width up to 342 m. About $\frac{3}{4}$ of the distance from the west end a shallow ridge separates the lake into two basins hereafter referred to as the West Basin and the East Basin (see Fig. 2). In general the morphometry of the two basins is similar, although the East Basin is not so deep. One might expect both basins to exhibit similar physical

TABLE 1. Significant morphometric data on Myers Lake

Depth	Area $m^2 \times 10^3$	% surface area	% volume below each depth	Stratum m	Volume $m^3 \times 10^3$	% volume
<u>West Basin</u>						
0	288	100	100	0-1	233	11.7
1	182	63.0	88.3	1-2	181	9.1
2	166	57.5	79.2	2-3	163	8.2
3	161	55.7	71.0	3-4	158	8.0
4	155	53.8	63.0	4-5	152	7.7
5	149	51.6	55.3	5-6	147	7.4
6	144	50.0	47.9	6-7	141	7.1
7	138	47.9	40.8	7-8	134	6.8
8	130	45.2	34.0	8-9	126	6.4
9	122	42.2	27.6	9-10	118	5.9
10	113	39.0	21.7	10-11	107	5.4
11	101	35.0	16.3	11-12	94	4.7
12	87	30.0	11.6	12-13	79	4.0
13	72	24.8	7.6	13-14	63	3.2
14	55	19.1	4.4	14-15	46	2.3
15	37	13.0	2.1	15-16	29	1.4
16	21	7.2	0.7	16-17	12	0.6
17	6	2.0	0.1	17-17.9	2	0.1
Total:					1,985	
<u>East Basin</u>						
0	91	100	100	0-1	71	21.0
1	53	58.0	79.0	1-2	40	12.0
2	40	44.0	67.0	2-3	39	11.4
3	37	41.0	55.6	3-4	36	10.7
4	35	38.5	44.9	4-5	34	10.0
5	32	35.6	34.9	5-6	31	9.1
6	29	32.0	25.8	6-7	27	8.0
7	25	27.5	17.8	7-8	23	6.7
8	21	22.8	11.1	8-9	18	5.4
9	15	17.1	5.7	9-10	12	3.7
10	10	10.5	2.0	10-11	6	1.8
11	3	3.5	0.2	11-11.9	1	0.3
Total:					338	
				Total Lake	West Basin	East Basin
Area ($m^2 \times 10^3$)				379	288	91
Volume ($m^3 \times 10^3$)				2,328	1,985	338
Max. depth (m)				17.9	17.9	11.9
Mean depth (m)				6.2	6.9	3.7
Mean/max. depth				0.35	0.39	0.31
Volume development				1.05	1.17	0.93
Max. depth (m)/Varea (ha)				2.91	3.31	3.94
Length of shoreline (m)				3,600		
Shoreline development				1.65		

and chemical characteristics, showing similar oxygen curves. This is true only in part. At times the East Basin shows a very ordinary clinograde oxygen curve. Under conditions of prolonged calmness the East Basin does develop a moderate oxygen maximum in the mid-metalimnion (see Table I, appendix). Since the long axis of the lake lies almost straight east and west, the prevailing "westerly" winds can sweep across the entire length of the lake. The full force of this action is felt at the east end, but because of the high bar separating the two basins the strong return current (undertow) is prevented from moving completely back into the West Basin. This concentrated turbulence in the East Basin during high winds very rapidly dissipates any oxygen

supersaturation in the metalimnion. In the summer of 1954 several winds of almost tornado velocity from the west even reduced considerably the oxygen concentrations in the West Basin. This is discussed at greater length later in the paper.

While the maximum depth according to the map is 17.9 m (59 feet) the deepest spot actually observed by the writer was about 17.5 m. Most of the samples from the summers of 1953 to 1955 were taken at station A on the map at a depth of from 16.5 to 17.5 m. Samples were taken in 1952 and part of 1953 at station B at a depth of 13 to 15.5 m. The East Basin has a maximum depth of 11.9 m (39 feet). The mean depth has been calculated as 6.2 m for the lake as a whole, 6.9 m for the West Basin, and 3.7 m for the East Basin.

The mean/maximum depth ratio indicates the character of the basin. A mean depth of $\frac{1}{3}$ the maximum depth indicates a basin of about the proportions of a cone. This ratio for Myers Lake is 0.35 (West Basin 0.39, East Basin 0.31). The nature of the basin is reflected also in the volume development ratio (3 times mean/max. depth). A value less than unity indicates that the lake basin walls are convex to the lake surface while a ratio greater than unity indicates concave slopes. The ratio for Myers Lake is 1.05. However, the West Basin has a volume development of 1.17, indicating moderately concave slopes, while the East Basin has a ratio of 0.93, indicating somewhat convex slopes.

These figures are somewhat misleading because of the large area of water above the shallow shelf less than 1 meter deep. In the West Basin about 3% and in the East Basin 5.4% of the total volume of water is contained above the shelf between the 0 and 1 meter contours. If calculations are made without including the volume of water just referred to, the mean/max. depth ratio becomes 0.59 for the West Basin and 0.51 for the East Basin, and the volume developments 1.7 and 1.53, respectively. This emphasizes first the divergence in the shape of the lower parts of the two basins and also the more box-like shape of the West Basin.

DISSOLVED OXYGEN AND OTHER PHYSICAL AND CHEMICAL CHARACTERISTICS OF MYERS LAKE

Oxygen profiles that are most indicative of the nature of the metabolic activities of a lake characteristically develop during the period of summer stagnation. Between the periods of fall and spring circulation all dimictic lakes show similar patterns of oxygen distribution, *i.e.*, with more or less equal amounts of oxygen (near saturation) at all depths.

Over 60 series of oxygen determinations on Myers Lake are available for the period 1952-1955. These cover fully both winter and summer conditions, including the early development of the metalimnetic oxygen maximum. These data are given in Tables A to D in the appendix and are shown graphically in Figure 3. Mean oxygen concentrations for the summers of 1952 to 1955 are given in Table 2.

The sub-surface oxygen maximum appeared first in the spring at a depth of 5 to 6 meters and slowly descended to a depth of 8 or 9 meters where it remained until the fall overturn. The maximum concentration varied from 12 ppm to over 20 ppm, with the highest observed value,

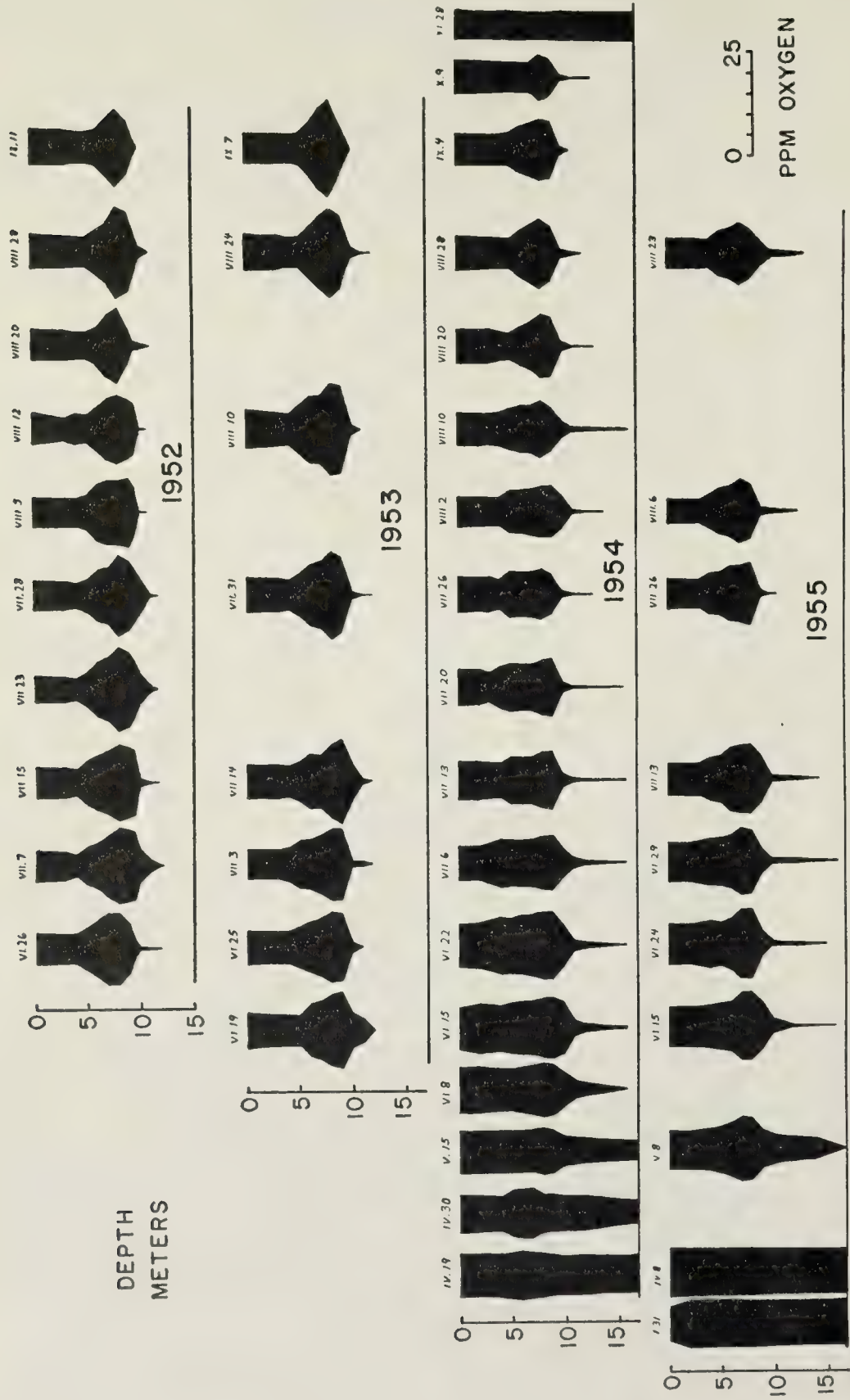


FIG. 3. Distribution of dissolved oxygen in Myers Lake, West Basin, 1952-1955.

TABLE 2. Mean summer oxygen concentrations
(ppm) from 0 to 12 m in West Basin

Depth (m)	Year*			
	1952	1953	1954	1955
0	7.40	8.27	8.93	7.91
1				
2			9.12	
3	6.93	8.06		7.77
4	6.62	7.67	9.42	9.54
5	8.56	9.25	10.60	11.22
6	11.89	13.60	11.60	13.32
7	15.18	16.24	12.29	15.71
8	18.35	19.98	13.98	15.08
9	15.42	18.49	13.55	6.18
10	3.93	4.32	6.42	1.57
11	0.83	0.58	1.98	0.81
12	0.04	0.05	1.06	0.75

* 1952: June 26-Aug. 28 (9 series)
 1953: June 19-Sept. 7 (9 series)
 1954: June 8-Sept. 4 (19 series)
 1955: June 15-Aug. 23 (7 series)

23.3 ppm, occurring on September 7, 1953. The oxygen gradient from the high oxygen region of the metalimnion into the low oxygen layers of the hypolimnion is frequently very steep. On July 15, 1952, the decrease was 13.7 ppm in one-half meter (9.5 m to 10 m). The oxygen deficit in the hypolimnion was less pronounced in 1954 than in the other years.

The distributional pattern of dissolved oxygen for 1952 is shown in Figure 4. The effect of the sinking thermocline (defined as the plane of maximum rate of decrease in temperature: Hutchinson 1957) on the oxygen content of the upper level of the metalimnion is very evident in the downward slope of the 8 ppm isoxygon, from a little below 4 m early in the summer to over 5.5 m by September. The lines for 10 and 15 ppm roughly parallel the 8 ppm isoxygon. Below the 2 peaks of oxygen production the upward slope of the lines reflects the development of the oxygen deficit in the hypolimnion.

It is evident from Figure 3 that the oxygen profiles show 4 rather distinct regions. The epilimnion contains a fairly uniform amount of oxygen varying from 85% to 110% saturation. Any greater accumulation of oxygen is precluded because the entire epilimnion is subject to wind-induced turbulence. Immediately below the upper boundary of the metalimnion, protected from the turbulence of the epilimnion, is a region of increased oxygen concentrations extending down to about 7 m. This zone is generally distinct from the region of greatest oxygen content at 8 to 9 m. The fourth zone is the hypolimnion, largely devoid of oxygen throughout most of the summer.

The two levels of metalimnetic oxygen concentrations were produced by two different populations of phytoplankton. Since the oxygen of the epilimnion was produced by a still different population of algae, this means that there were three distinct producing populations of algae. This multilevel photosynthesis in Myers Lake is one of the significant factors contributing toward the development of the high gross production in the lake as a whole.

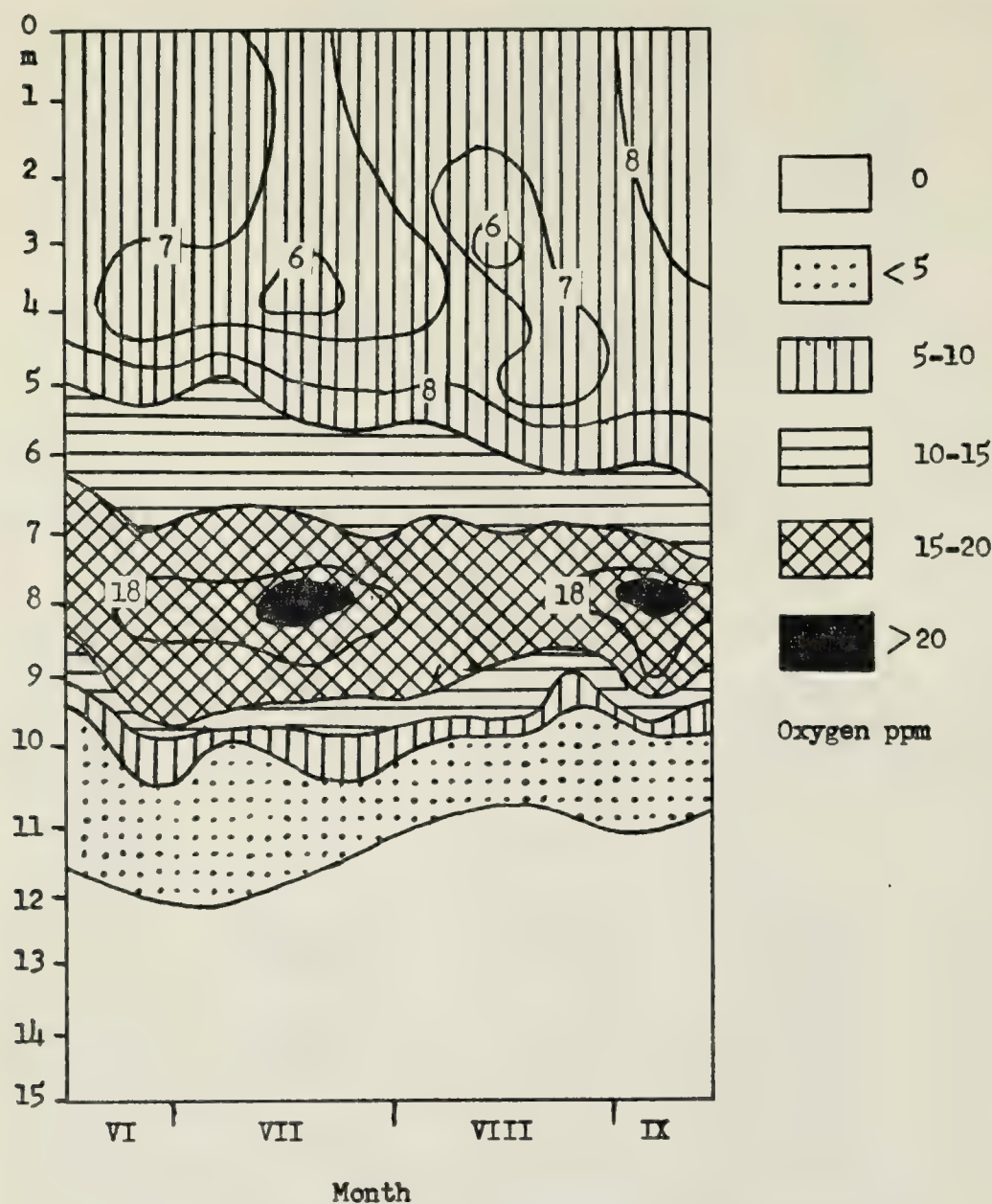


FIG. 4. Oxygen distribution in Myers Lake, West Basin, 1952.

The metalimnion of Myers Lake (see Tables E to H in the appendix) averages 6 to 7 m thick and is fairly high, beginning above 3 m early in the summer and moving down to 4 or 5 m by September. A high thermocline increases the thickness of the zone of protected water in which a large concentration of oxygen can accumulate. The mean summer temperature of the West Basin for the years 1952-1955 was 17.95°C (Table 12) while the mean temperature of the East Basin during the summer of 1955 was 20.29°C (Table 14).

The relatively greater effect of the wind in the East Basin is implied by the higher mean temperature, but is more adequately assessed by comparing the summer heat incomes of the two basins and the amount of work expended by the wind in mixing this heat in the lake (Birge 1916).

The summer heat budget for the East Basin during 1954 (to July 22) was 6577 Cal/cm², which required 216.19 g·cm/cm² of work to distribute this heat through the lake at a rate of about 30.4 Cal/g·cm. During the same period the summer heat income of the West Basin was 9601 Cal/cm² distributed by 343.54 g·cm /cm² of work, or 27.9 Cal/g·cm. This variance in the effect of the wind in the two basins was even more pronounced in the spring of 1955. On June 15, 1955, the wind-distributed heat in the East Basin amounted to 43.4 Cal/g·cm while the rate for the West Basin was 36.3 Cal/g·cm. Between June 15 and August 24, 1955, the effect of the wind was almost identical in both basins, 18 Cal/g·cm, which indicates only moderate wind action during this period (<0.3 Cal/g·cm/day) as well as approximately equally effective stratifications in both basins.

Summer transparency ranged from 3.2 to 6.1 m (Tables A - D, appendix) with a mid-summer average of about 4.8 m. The transparency was highest in 1952 and lowest in 1954. Variation in transparency is related to the abundance of phytoplankton in the epilimnion as well as the specific conditions of light intensity and surface disturbance at the time of the measurement. Later measurements with a photometer showed 1% of the surface illumination present at 7.9 to 8.1 m in the East Basin (Table J, appendix).

The following data on the range of concentrations of chemical substances during stratification are presented merely to characterize Myers Lake. These data have been compared with data for other lakes in Northern Indiana (unpublished data) and with a table summarizing the concentrations of important mineral constituents in natural fresh waters presented by Krauss (1953).

One of the best single indices of the concentration of dissolved chemical substances in natural water is specific conductance, a high value indicating a high concentration of dissolved electrolytes. For Myers Lake the specific conductance varied from 190 to 250 mho x 10⁻⁶ at 18° C in the trophogenic zone, with somewhat higher values for the hypolimnion. This is lower than for most lakes in Northern Indiana.

Inorganic phosphorus ranged from 1 to 14 µg/L with higher concentrations near the bottom. The mean value for the metalimnion during the summer of 1954 was about 4 µg/L. One sample analyzed for calcium showed 27.3 ppm at the surface and 35.2 ppm at 8 m, both moderately low values. Methyl orange alkalinity varied from 114 to over 200 ppm, with the highest values in the hypolimnion and the lowest values in the trophogenic zone. The pH ranged from as high as 8.7 in the trophogenic zone, dropping sharply in the hypolimnion to near 7 at the bottom.

Myers Lake fits favorably in the mesotrophic category of Yoshimura (1938). Certain of the alga species also indicate mesotrophy (Teiling 1955 and Rawson 1956). Chemically (qualitatively) the lake favors the growth of bluegreen algae, and thus the tendency is toward eutrophy, but the low level of dissolved nutrients limits the total production of especially the epilimnetic flora. Morphometrically the lake basin tends toward oligotrophy. Because the peculiar combination of factors permits photosynthesis at at least three distinct levels (as alluded to above) the gross production of Myers Lake is high.

THE ECOLOGY OF OXYGEN PRODUCTION

In order to understand the formation of the metalimnetic oxygen maximum, a knowledge of the rates of oxygen production, especially in the metalimnion, is necessary. The oxygen involved in the metalimnetic maximum must be produced in that region and not accumulated from some other source. It is also desirable to evaluate the rate of oxygen production by specific phytoplankters under the specific conditions that exist in the metalimnion.

There are two ways of evaluating oxygen production: 1) gross production can be considered as a function of the lake as a whole; 2) the rate of oxygen production can be considered from the view of understanding the process of photosynthesis, either *per se* or as contributing toward an understanding of phytoplankton ecology. In view of the problem at hand, it seems wise to include both considerations. Data on gross production will enable one to compare a lake with a metalimnetic oxygen maximum with other types of lakes where production is known, while specific production rates in Myers Lake will lead to a better understanding of photosynthesis relative to the range of the many environmental factors as they exist in nature.

Since any changes that occur in the oxygen content of the metalimnion of a lake during stratification are the result of shifts in the balance between respiration and photosynthesis (except for changes due to eddy diffusion), the net production (*i.e.*, gross production minus respiration) is also important and will be considered in relation to changes which occurred in Myers Lake during 1954.

Primary production has been expressed by workers variously as weight or volume of oxygen produced, carbon dioxide or carbon consumed, weight of glucose produced, etc. Results in the present paper are expressed as micrograms of oxygen or equivalent weight of carbon. Micrograms O_2 are easily converted to micromoles O_2 by dividing by 32, to micrograms glucose by multiplying by 0.937, and to micrograms C by multiplying by 0.375 (P.Q.=1).

Gross oxygen production

Photosynthesis was measured with the light-dark bottle method on several different occasions for varying periods of time. Five series of bottles were exposed for a short period of daylight, while two experiments lasted over 2 days. Steemann Nielsen (1952) felt that long-term exposures gave photosynthesis readings too high, but Ryther (1956b) challenges Steemann Nielsen's criticism by stating that his own experience has indicated that such experiments give readings that are too low. The two-day exposures in the present investigation gave lower results than the short-term, daylight exposures. Verduin (1956b) prefers periods of 2-6 hours. The limits of error used in the present calculations are based on Ryther's (1956b) evaluation of the accuracy of the Winkler method of oxygen titration.

Daily rates of oxygen production were calculated by assuming a 12-hour day. Hourly rates determined from the short-term exposures will not be uniform throughout the entire 12-hour period. From an examination of Figure 4 of Ryther (1956a) it was estimated that the photosyn-

thetic rates observed during midday (0900-1600 hours) would account for roughly 85% of the total daily production. Edmondson (1956) also mentions the 85% approximation. Hourly rates of oxygen production, determined from the short-term photosynthesis runs made during the midday hours, were used to calculate daily production by the following equation:

$$\mu\text{g O}_2/\text{L/hr} \times 12 \times 0.85 = \mu\text{g O}_2/\text{L/day} \quad (5)$$

Daily production can be derived from the long-term exposures directly. Daily gross production estimates are given in Table 3.

TABLE 3. Daily gross oxygen production
($\mu\text{g O}_2/\text{L}$) in West Basin

Depth m	Aug. 10 1954	Aug. 26 1954	Aug. 28 1954	Sept. 2 1954	Sept. 4 1954	Aug. 29 1955	Sept. 1 1955	Mean
0	286	293	(329)	714	627	510	816	510
2	510	337	329	663	657	(459)	(704)	522
4	510	107	357	238	373	408	592	369
5	(877)	222	169	136	329	510	510	393
6	1244	187	357	833	508	850	184	594
7	(1214)	(169)	(348)	(816)	(919)	1377	245	726
8	1183	151	338	799	1329	663	816	754
9	428	195	141	17	164	204	184	190
10	326	266	33	85				
Limits of error	143	32	34	122	108	122	143	101
Time (hours)	5	51	49.5	6	6.83	6	5	
Transparency:								
disc (m)	3.6	4.2	4.1	4.2	5.0			
1% level (m)						9.0	8.5	

Note: figures in () are the averages of the values immediately above and below.

There are two levels of high oxygen production. The first occurs in the epilimnion. As the mean values show, the highest production is not right at the surface, but at a depth of 2 m. This is probably due to the inhibitory effects of high light intensity. Photo-inactivation of chlorophyll is reviewed thoroughly by Rabinowitch (1945, 1951). This phenomenon has been observed in the surface waters of lakes by several investigators, *e.g.*, Schomer and Juday (1935) and Edmondson (1956).

Due to circulation caused by wind-induced eddy turbulence, one would expect to find a rather homogeneous population of plankton in the epilimnion. Hence it seems likely that the decrease in production down to 5 m is due to the diminution of light.

Immediately below the thermocline production rates rise to almost 50% higher than the highest mean rate in the epilimnion, reaching maximum levels at 7 and 8 m. Production of oxygen decreases at 9 and 10 m. It is unlikely that any appreciable photosynthesis occurred below 10 m, although on two occasions there was still considerable production at this depth. In figuring mean rates only values down to 9 m were used since there was not a full series available at 10 m, but the occasional significant production below 9 m must be recognized. The writer has no

explanation for the two apparently anomalous cases where production at 10 m exceeded that of the 9 m stratum.

Net oxygen production

The free oxygen that is measured is the accumulated surplus over that utilized in respiration. If the oxygen consumed by a planktonic community over a 24-hour period just equaled that produced by the photosynthetic members of the community during the daylight hours, there would be no change in the oxygen content from day to day, measured at the same time each day. In natural situations this almost never happens. There are changes in populations as well as variations in light and temperature which result in continual change in the rates of both photosynthesis and respiration. As a result the net photosynthesis may reflect either a gain or loss of oxygen from day to day.

Data from five of the experiments were suitable for the calculation of net production rates (Table 4). The various strata may have a net

TABLE 4. Net daily production
($\mu\text{g O}_2/\text{L}$) in West Basin

Depth m	Aug. 26 1954	Aug. 28 1954	Sept. 2 1954	Sept. 4 1954	Aug. 29 1955	Mean
0	-22	(-53)	34	276	270	101
2	-58	-53	463	60	(19)	.86
4	-213	96	-362	91	-232	-124
5	100	-29	-904	-22	-250	-221
6	4	-272	393	226	250	120
7	(-76)	(-13)	(336)	(919)	937	421
8	-155	246	279	1329	343	408
9	115	131	-2103	164	-1128	-564
10	-152	-103	-395			

Note: figures in () are the averages of the values immediately above and below.

oxygen surplus at times and at other times may actually lose oxygen. The figures for mean net production show highest rates right at the surface and at 6-8 meters, the latter being more than four times greater than the former. The net production represents oxygen that can accumulate and yield a supersaturation. The excess of the epilimnion is generally dissipated through turbulence, but the oxygen of the metalimnion is well sealed off from epilimnetic disturbance by a strong thermocline.

The cumulative effect of the variations in net production is readily discernible in the weekly oxygen analyses reported in the appendix (Tables A-D). The weekly oxygen gain or loss (mg/L) plotted cumulatively for the strata of the metalimnion (5-10 m) for 1954 is shown in Figure 5.

Certain trends are evident. All strata gained rapidly the first several weeks, and all except the 10 m stratum lost about the same amount between June 22 and June 29. This was due to a severe wind storm of almost tornado velocity that produced turbulent disturbances presumably

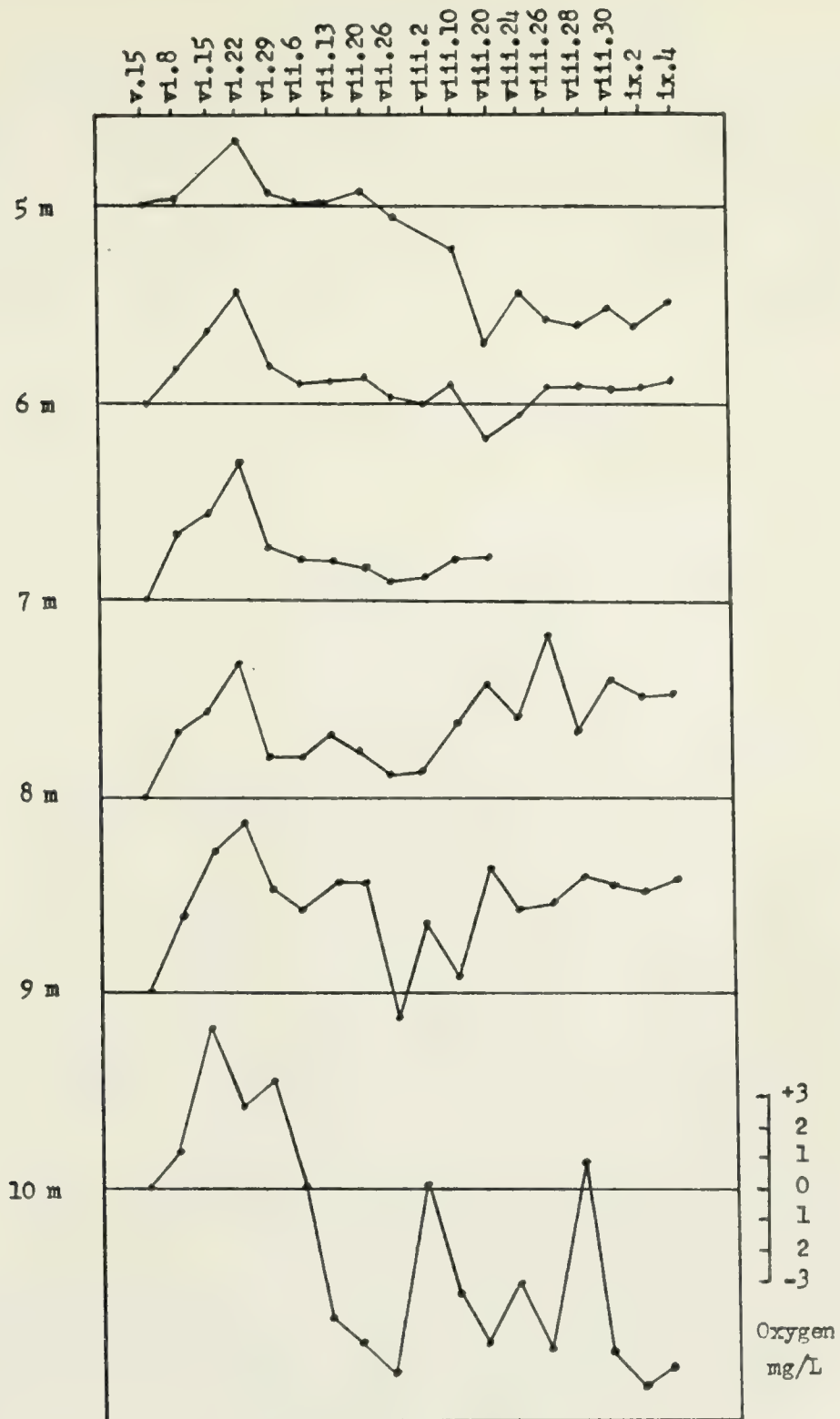


FIG. 5. Cumulative gain or loss of oxygen in the various strata of the metalimnion during 1954. Initial values on May 15 are the reference points to which subsequent changes are related.

down as far as 9 m. There is an obvious downward slope of the 5 m layer that reflects the lowering of the bottom of the epilimnion during the summer. The 6 and 7 m strata appear to maintain themselves fairly steadily throughout most of the summer. There is a gradual increase in the net accumulation of the 8 m stratum. The 9 m stratum fluctuates widely, being very close to the lower limit of adequate light for photosynthesis, while the 10 m layer reflects the gradual loss of oxygen characteristic of water below the euphotic zone. And so the more or less consistent production of a net surplus of oxygen in the 8 m stratum is another factor that makes possible the high accumulation of oxygen that occurs there.

Total daily production

Total daily production calculated from the mean rates of gross and net production integrated for the volume of the euphotic zone (0-9 m), is shown in Table 5.

TABLE 5. Total daily production, West Basin,
Meyers Lake, based on the mean values
reported in Tables 3 and 4

Strata m	Volume m ³ x 10 ⁵	Gross production			Net production		
		kg O ₂	kg C	%	kg O ₂	kg C	%
0 - 2	3.6	185.8	69.7	26	33.8	12.7	27
2 - 4	3.2	142.7	53.5	20	-6.1	-2.3	
4 - 5	1.5	57.2	21.4	8	-18.5	-6.9	
5 - 6	1.5	74.1	27.8	10	-7.5	-2.8	
6 - 7	1.4	92.4	34.7	13	37.9	14.2	30
7 - 8	1.3	96.2	36.1	14	54.0	20.3	43
8 - 9	1.3	61.4	23.0	9	-10.1	-3.8	
Totals	13.8	709.4	226.2		83.5	31.3	
g/m ²		3.94	1.48		0.46	0.17	
Mean production of trophogenic zone (0-9 m), g/m ³		0.51	0.19		0.060	0.023	

The mean gross production of the West Basin of Myers Lake is 709.4 kg O₂ or 266.2 kg C per day. There are no data available on the productivity of the East Basin. In determining an areal approximation of production the area within the 0-1 m contour (A₀₋₁) has been omitted, because during the summer this zone fills up completely with both submergent and emergent vegetation and hence does not function as a part of the limnetic zone. The effective area then becomes the area of the 1-m contour projected to the surface. If the total gross production is related to this area, the production rate becomes 3.94 g O₂/m²/day or 1.48 g C/m²/day.

Verduin (1956a) concluded that most lakes show daily yields of 4.8 to 6.4 g O_2/m^2 . Nygaard (1955) has shown the productivity of five Danish lakes to vary between 0 and 11.1 g $O_2/m^2/day$, with a yearly average for the five lakes of 0.2, 0.62, 0.66, 2.0, and 2.75. Rodhe (1958) observed a range of 0.07 to 2.2 g C/ m^2/day in seven lakes in Sweden. Riley (1956) has estimated gross production rates of 0.23-1.70 g C/ m^2/day for Long Island Sound, and more recently (Riley 1957) has made estimates of 0.09 to 0.89 g C/ m^2/day for the Sargasso Sea, while Ryther and Yentsch (1958) have published values of 0.20 to 1.00 g C/ m^2/day for the continental shelf area off New York (P.Q.=1.25). Thus the productivity of Myers Lake is within the general range given for both fresh water and marine environments.

The mean gross production of the trophogenic zone (0-9 m) is 0.5 g $O_2/m^3/day$ (0.19 g C). This rate is calculated by dividing the total production by the volume of limnetic water from the surface to 9 meters. The volume of hypolimnetic water was not included because of lack of data regarding respiration values.

There is a mean net production of 0.46 g $O_2/m^2/day$ (0.17 g C) at a mean rate of 60 mg O_2/m^3 in the trophogenic zone. The strata between 2 and 6 m show a general net loss of oxygen. This layer represents the bottom of the epilimnion and the upper portion of the metalimnion. The two zones of positive net production are shown clearly in the table.

Photosynthesis and light intensity

Light intensity is a major factor producing vertical variations in photosynthetic rates. In Myers Lake only total illumination was measured. The depth at which surface illumination has been reduced to 1% has been considered the lower limit of the euphotic zone (Ruttner 1953). In 1954 only Secchi disc readings were available (see Tables A-D, appendix). There have been many attempts to convert Secchi disc readings to the 1% level of light intensity. Yoshimura (1938) used a factor of 1.2 (in his 1935 paper he had used 1.5); Riley (1941) used a factor of 3; while Verduin (1956a) obtained a factor of 5 for Lake Erie. Photometer readings in 1955 indicated that the 1% level varied from 7.9 m to 9.0 m, with a mean value of 8.46. Unfortunately only one simultaneous test was made with the Secchi disc and the photometer. The disc reading was 4.9 m, while the photometer showed the 1% level at 8.2 m. This gives a factor of 1.67. It is probable that a single factor will not give consistent results under all conditions. It is obvious from Table 3 that on the date of the lowest Secchi disc reading (viii.10.54) there occurred the highest production in the 9 and 10 meter strata. On that date the 1% level was certainly at 9 m or deeper which would give a conversion factor of *ca* 2.5. It seems likely that the factor for Myers Lake might vary from 1.5 to perhaps 2.5 depending on the circumstances under which the disc readings are obtained.

Myers Lake is a moderately clear lake (see Fig. 6), with a mean extinction coefficient measured to the 1% level ($k_{1\%}$) of 0.54 (Table J, appendix). The $k_{1\%}$ index is used because it seems to give a better appraisal of conditions in the lake as a whole than any other form of the

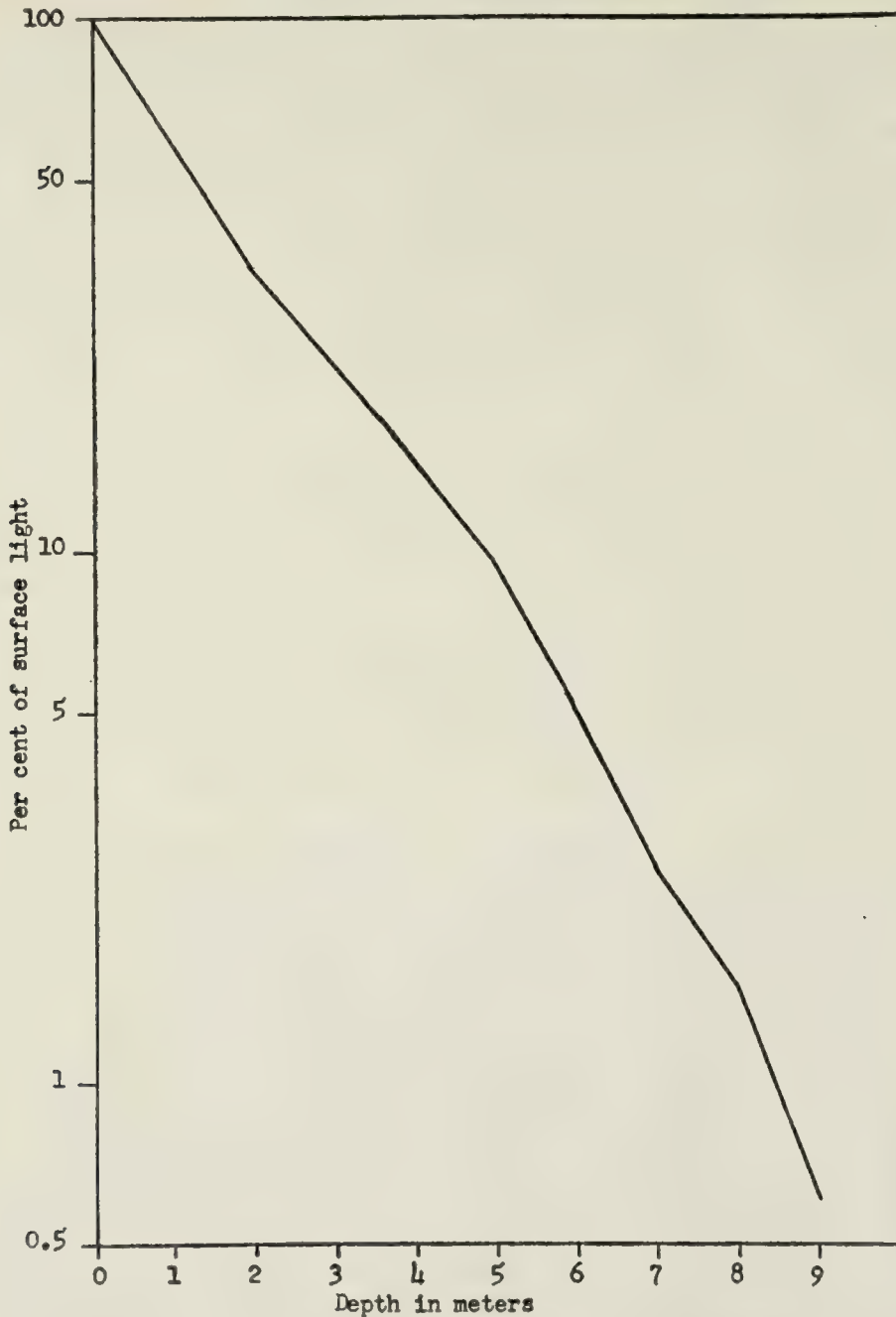


FIG. 6. Mean light transmission curve, West Basin.

extinction coefficient. This index is determined from the usual form of the equation (Clark 1939)

$$\frac{I_m}{I_o} = e^{-kL_m}$$

where I_o is the light intensity at the surface (100%), I_m is the light intensity at depth m (1%), L is the thickness of water to depth m (the depth of the 1% level in meters), and k is the extinction coefficient. The values of $k_{1\%}$ for some of the lakes of Wisconsin reported by Birge and Juday (1932, Table 1) ranged from 0.26 to 4.61. The few Indiana lakes for which data are available range from 0.63 to 1.64. The East Basin

of Myers Lake has a mean $k_{1\%}$ of 0.59, slightly less transparent than the West Basin.

The relation between the extinction coefficient and the Secchi disc reading is sometimes expressed as:

$$k = \frac{C}{D}$$

where D is the Secchi disc transparency in meters, and C is an empirically determined constant (Edmondson 1956). Most recent workers follow Poole and Atkins (1929) who determined C to be 1.70 for oceanographic work. In the one example in Myers Lake referred to above when simultaneous tests were made, D was 4.9 and $k_{1\%}$ was 0.56 (1% at 8.2 m) which makes C equal to 2.74. With a value of $C = 1.70$, the disc reading should have been 3 m. It seems that C is not a constant, in some cases, but might better be expressed as a range within which the extinction coefficient might be inferred from the disc transparency.

Taking the mean depth of the 1% level as 8.4 m it is obvious from Table 3 that there is some photosynthesis occurring below this level. This is also reflected in the oxygen analyses of the lake, particularly during 1954 and 1955 (Tables C and D, appendix). If we assume that the hypolimnion is fairly stable and relatively free from vertical turbulence, the frequently increased oxygen content of the 9-12 meter strata (*e.g.*, on August 23, 1955) is at least partially the result of actual production due to increased light penetration at that level, although all is below the 1% level. The explanation lies in the presence of an alga, *Oscillatoria agardhii*, which can carry on photosynthesis at that low level of light intensity. It is worth noting that Nygaard (1955) has recently reported photosynthesis at less than 1% illumination in some Danish lakes.

Maximum oxygen production in the metalimnion occurs in the 6-8 m stratum with light intensities below 5% of surface illumination. It will be shown later that there are two distinct populations of algae in the metalimnion: one group exhibits its maximum production of oxygen in the 6-7 m level with about 2-5% light intensity, while the other population produces the maximum amount of oxygen at 8 meters with about 0.5 to 2% of surface intensity. The decrease in oxygen production below the 8-meter maximum seems to be due to light decrease, since the actual plankton population usually increases below this depth for a few meters. There was no evidence of senescence in the algae at 9 or 10 meters, so evidently there was still adequate light present at this depth to maintain minimum metabolic activities. It is possible, however, that *Oscillatoria agardhii* is able to carry on some type of chemotrophic assimilation of carbon under conditions of very low light intensity. Hydrogen sulfide, known to occur in the hypolimnion of Myers Lake during stratification, is the chief energy source for *Beggiatoa*, a colorless Myxophycean-like organism (Fogg 1953). Sulfur droplets have been found in the cells of some *Oscillatorias* (Hinze 1903). The similarity of the *Oscillatorias* to certain of the sulfur and iron bacteria (?) has been discussed by Fritsch (1945). The prospect of *Oscillatoria agardhii* being facultatively chemolithotrophic (see Fogg 1953) is an intriguing possibility, but was not investigated during the present study on Myers Lake. In passing,

it might be mentioned that most of the deep metalimnetic oxygen maxima reported in the literature have been associated with bluegreen algae.

One of the most interesting facts shown in Table 5 is that 73% of the total mean net production of oxygen occurs in the metalimnion. It is this fundamental fact that makes possible the development of a metalimnetic oxygen maximum. It is necessary to examine the phytoplankton responsible for this net surplus and to try to determine the relationship between quantity of phytoplankton present and photosynthesis rates.

Phytoplankton and production

The simplest way of expressing the quantity of algae present is a direct count of individual organisms. This presents certain difficulties because a) not all organisms are equivalent oxygen producers, and b) nanoplankters are enumerated with great difficulty. Part of this problem can be overcome by devising phytoplankton units which contain equivalent amounts of each species, *i.e.*, equal cell volumes or chlorophyll content. The system used by the writer, patterned after Chandler (1940) and Tucker (1957), is as follows:

<i>Oscillatoria, Melosira, Aphanizomenon</i>	300 micra/unit
All Chroococcales	2 cells or colonies/unit
<i>Asterionella, Fragilaria, Cyclotella</i>	8 cells/unit
<i>Dinobryon</i>	5 cells/unit
<i>Ceratium</i>	1 cell/unit

TABLE 6. Total phytoplankton units per liter (1954) ($\times 10^5$)

Depth m	April		May 15	June					July	
	19	30		8	11	15	22	29	6	13
0	2.4	1.6	2.0		6.2			0.5	0.7	0.5
2										
4	1.9	1.1	1.7					2.8	1.2	1.0
5										
6	8.1	7.8	2.3	0.4	1.0			1.0	0.6	1.5
7				0.8						
8	5.7	19.5	15.1	4.4	2.9	3.6	0.9	1.6	0.6	2.0
9			27.4	12.9						14.5
10	3.3	2.7	9.4	25.5	36.8	26.4	22.1	44.6	14.1	10.6
11										8.3
12	2.3		2.0	9.1	7.1	10.5	10.3	3.4	4.9	3.0

Depth m	July		August					September	
	20	26	2	10	20	24	28	2	4
0	1.4		1.0			1.5	1.5	1.8	1.8
2						1.5	2.1		1.2
4	0.2		2.1			3.4	1.7	0.6	0.7
5						2.4	1.1	1.5	0.4
6	1.5		3.3			17.0	7.9	9.2	4.8
7					3.0				
8	1.1	5.4	3.5	13.2	7.5	4.2	3.2	7.3	5.5
9	16.5	27.1	33.2	32.7	24.5	22.8	11.6	21.5	72.2
10	9.2	5.4	12.3	13.6	21.0	10.1	17.8	42.1	44.9
11	11.1	6.4	8.1		2.7				
12	2.3	2.4	2.2	4.2		2.1	1.4	2.5	0.9

The least reliable of these units is admittedly the Chroococcales, but this is excused on the basis that they occur chiefly in the epilimnion and scarcely enter the picture as far as photosynthesis in the metalimnion is concerned. Table 6 gives the total units of phytoplankton per liter at selected depths during the summer of 1954. Using the figures for the days on which photosynthesis was measured, the rate of oxygen production per 10^6 phytoplankton units can be calculated at each depth (Table 7).

TABLE 7. Oxygen production related to number of
phytoplankton units ($\mu\text{g O}_2/10^6$
phytoplankton units/day)

Depth m	Aug. 10 1954	Sept. 2 1954	Sept. 4 1954
0		40	35
2			55
4		40	53
5		9	82
6		9	11
8	9	11	24
9	2	< 1	< 1
10	2	< 1	

There are obviously higher rates in the epilimnion where higher temperatures and higher light intensities prevail. The rates drop at the top of the metalimnion, then rise at the 8 meter level, after which they drop off abruptly. It is doubtful if such an attempt to correlate production with numbers of organisms in mixed populations is too useful because there are too many unanswered questions concerning the metabolism of the various species under different conditions of temperature and light such as prevail in vertical series like these. Also, merely to try to equate certain numbers of one species with a certain number of another on the basis of approximate size or estimated cell volume does not assure that these units are equivalent oxygen producers under identical conditions.

Verduin (1952) favors a volume-based photosynthetic rate. In this paper Verduin cites rates for algae ranging from 1 to 18 $\mu\text{-moles O}_2/10^{10} \mu^3/\text{hr}$. In later papers (1953, 1956a), he used a mean value of 0.4 $\mu\text{-moles}/\mu\text{L}/\text{hr}$ (this is equivalent to $13\mu\text{g}/10^{10} \mu^3/\text{day}$). In Myers Lake most of the phytoplankton of the metalimnion was of the filamentous type for which the volume could be rather accurately determined; hence the volume-based rates for that region only are given (Table 8). These rates fall within the range given by Verduin, again showing higher rates at 8 meters and much lower rates below this level.

Probably the most accurate means of relating photosynthesis to quantity of algae in heterogeneous natural populations is by chlorophyll content. Only one chlorophyll analysis was run on a day that photosynthesis was also being tested. The results are summarized in Table 9. The column headed AZ is the assimilation quotient of Gessner (1943) expressed as $\text{g CO}_2/\text{hr}/\text{g chlorophyll}$. The mean AZ, 0.8, is lower than mean figures

TABLE 8. Oxygen production related to volume of phytoplankton ($\mu\text{g O}_2/10^{10} \mu^3$ plankton/day)

Depth m	Aug. 10 1954	Sept. 2 1954	Sept. 4 1954
6		18	21
8	13	19	46
9	3	<1	<1
10	3	<1	

TABLE 9. Oxygen production related to quantity of chlorophyll, Sept. 4, 1954

Depth m	$\mu\text{g O}_2/\text{L/day}$	$\mu\text{g chlor.}/\text{L}$	$\mu\text{g O}_2/\mu\text{g chlor.}/\text{day}$	AZ
0	627	45	14	1.4
2	657	50	13	1.3
4	373	60	6	0.6
5	329	60	5	0.5
6	508	100	5	0.5
8	1329	145	9	0.9
9	164	735	<1	0.02
		Mean	8.3	0.8

given by Gessner. Perhaps this is indicative of the behavior of algae in media of low nutrient levels as in Myers Lake. Deep-water flora might be expected to have a low AZ ration also. With a P.Q. of 1 the AZ is equal to the hourly rate of oxygen production per unit of chlorophyll ($0.8 \mu\text{g O}_2/\text{hr}/\mu\text{g chlor.}$ or $0.3 \mu\text{g C/hr}/\mu\text{g chlor.}$). This rate is considerably lower than those of Ryther and Yentsch (1957, 1958) who arrived at a mean value of $3.7 \text{ g C/hr/g chlorophyll}$, and Shimada (1958) who estimated a rate of $4.24 \text{ mg C/hr/mg chlorophyll}$.

It is interesting to note that in every way we have tried to relate photosynthesis to phytoplankton (Tables 7-9), the rates at 8 m have been higher than those immediately above and below the depth. Thus we see that the phytoplankton of the 8-meter stratum, in spite of the lower temperature and reduced illumination that exist there, not only has an unexpectedly higher rate of photosynthesis but also occurs in tremendous concentrations.

THE PHYTOPLANKTON OF MYERS LAKE

Myers Lake is essentially a bluegreen-diatom lake. The dominant form by far is *Oscillatoria agardhii* which is present the year round. Diatoms (especially *Melosira*) constitute the next most prominent group. Various filamentous and colonial Cyanophyceae occur regularly, and *Ceratium hirundinella* and *Dinobryon sertularia* are present at times in large num-

bers. Only rarely, however, with the exception of the two species just named, do phytoplankters other than bluegreen algae or diatoms appear.

There is a pronounced vertical stratification of the phytoplankton during the period of thermal stratification in the lake. The flora of the epilimnion consists chiefly of Cyanophyceae such as *Gomphosphaeria wichurae*, *G. lacustris*, *Anacystis limnetica*, and *Anabaena circinalis*. Due to settling, these forms are also found to some degree in the deeper waters. *Ceratium* and *Dinobryon* have been found at all depths, but, since the role they play in photosynthesis is not known, they will not be considered further. Rarely one of the *Volvox* species would appear, as well as infrequent desmids, such as *Staurostrum*, but none in sufficient number to play an important part in the total metabolism of the community. At times what appeared to be a small species of *Chroococcus* was fairly abundant, but since it did not make up a very large percentage of the total volume of plankton present, it was disregarded. Phytoplankton was never too abundant in the epilimnion (see Table 6), rarely exceeding 3×10^5 plankton units per liter and often less than 0.5×10^5 units, which is the lower limit of sensitivity of this method of plankton counting.

This sparseness of the epilimnetic plankton and the resulting increased transparency is a significant factor in the development of the deep-water plankton that produces the metalimnetic oxygen maximum. The writer has no explanation for the low population density of the epilimnion unless it is a result of the low level of nutrients. Reference has already been made to the low dissolved phosphorus concentrations, especially in the epilimnion. The phosphorus content of Myers Lake is low compared with data from lakes and rivers compiled by Chu (in Krauss 1953). It is interesting to note that two species occurring in Myers Lake (*Dinobryon* and *Asterionella*) were observed by Rodhe (1948) to survive well experimentally in low concentrations of phosphorus. There is a growing body of evidence that phosphorus is an important limiting factor (reviewed by Hutchinson 1957).

Rodhe (1948) feels that plankton algae grow best within an *optimal range* of concentration or intensity of environmental factors. This optimal range is bounded by maximum and minimum values called, respectively, the *upper limit optimum* and *lower limit optimum*. Within the optimal range, growth of the organism is more or less proportional to the concentration or intensity of the factors involved, except that for a few factors (e.g., temperature) there is an *optimum level* which produces maximum growth. Above the upper limit optimum an increase in the factor no longer produces a corresponding increase in growth and/or may actually inhibit growth. Similar results occur when the environmental factors are reduced below the lower limit optimum. The optimal range for any given factor may vary considerably from species to species.

Thus, if the concentration of P is below the lower limit optimum for a particular species, that species will likely not survive at all. It is generally agreed that the green algae have a rather high lower limit optimum for phosphorus — $20 \mu\text{g/L}$ according to Rodhe (1948). This would explain the general absence of the Chlorophyceae from Myers Lake.

Because it has been virtually impossible so far to culture planktonic Cyanophyceae in controlled nutrient solutions, their mineral requirements

are only imperfectly known. Pearsall (1932) observed that the bluegreen algae show a general correlation with high organic matter and have the ability to grow rapidly in minimal quantities of nitrate and phosphate. Hutchinson (1944) showed that bluegreen blooms develop in late summer when the free inorganic nutrients are practically all exhausted. Gerloff *et al.* (1950), reporting on their attempts to culture planktonic species of bluegreen algae, indicated success only with *Coccochloris peniocyctis*. In their experiments they found that a "surprisingly low" concentration (0.45 ppm) of phosphorus still produced maximum growth. More recently the same workers (Gerloff and Skoog 1954) demonstrated that in solutions containing 0.4 ppm or more the yield of *Microcystis aeruginosa* remained constant, but that the P content of the cells increased fourfold with increasing phosphorus in solution. In solutions of 0.25 ppm P or less the cellular P remained constant, but the total production decreased with diminishing amounts of phosphorus in solution. There is evidence, then, that the Cyanophyceae in general are more tolerant of low phosphorus levels than other groups of algae that have been studied (except for some of the Dinophyceae that are inhibited by P concentrations much above 2 or 3 mg/L).

The flora of the metalimnion resolves itself into two rather distinct populations. The upper community extends down to 8 or 9 meters, reaching its maximum development at about 6 meters. It is composed chiefly of *Aphanizomenon flos-aquae* and *Melosira* sp. *Aphanizomenon* occurred at a higher level than *Melosira*, even getting into the epilimnion on some occasions. *Melosira* was the second most abundant phytoplankter in the lake, on one date amounting to 1,390,000 units/liter (viii.24.54; 6 m). Throughout most of the summer this *Aphanizomenon-Melosira* community was present but did not reach an appreciable size until August and September. However, the metabolic activity of algae at these levels is apparent from the increased oxygen content just below the upper level of the metalimnion (Fig. 3). There is a decided increase in the rate of production of oxygen at 6 meters, as high as 16.1 ppm (August 10, 1953). Early in the summer (May and June) *Asterionella* and *Fragillaria* probably played significant roles in the production of the upper part of the metalimnion.

The lower population of the metalimnion consists almost entirely of *Oscillatoria agardhii*. The quantitative distribution of this plankter during 1954 is given in Table 10. In the early stages of thermal stratification *O. agardhii* was distributed somewhat uniformly vertically in the lake, but with the warming of the surface waters the alga gradually disappeared from the epilimnion and developed extensive concentrations in the lower metalimnion at 8-10 meters. Since the highest oxygen concentrations appeared consistently at 8-9 meters, it seems certain that *O. agardhii* is the dominant agent responsible for this oxygen maximum.

Oscillatoria agardhii exhibits a wide range of environmental tolerances existing as ecotypes adapted to quite a variety of habitats. Specimens in the Cryptogamic Herbarium of the Chicago Natural History Museum have been collected from quarries, gravel pits, streams, ponds, and lakes at various depths. Problems in the distribution of *O. agardhii* are beyond the scope of this paper, except that it might be noted that it is

TABLE 10. Distribution of *Oscillatoria agardhii*
during 1954 ($10^9 \mu^3/L$)

Depth m	April		May 15	June					July	
	19	30		8	11	15	22	29	20	26
0	1.39	0.92	1.20	0						
4	1.11	0.64	0.82	0						
6	4.78	4.57	0.91	0						
7				0.23						
8	3.34	11.51	4.58	1.92	1.24	0.35	0.19	0	0.29	0.81
9			14.91	7.11						8.52
10	1.92	1.57	2.70	15.10	21.64	15.56	12.58	26.25	8.20	6.25
11										4.80
12	1.25			5.37	4.16	6.16	6.06	2.01	2.90	1.79

Depth m	July		August					September	
	20	26	2	10	20	24	28	2	4
4									
5								0.20	
6									0.13
7					0.18				
8	0.52	3.19	1.54	7.77	2.67	0.76	0.17	2.34	1.79
9	9.71	15.96	19.08	19.23	13.23	12.45	4.59	12.28	42.37
10	5.43	3.19	7.24	7.98	11.81	5.62	9.81	24.81	26.42
11	6.53	3.80	4.79		1.41				
12	1.33	1.42	1.31	2.44		1.12	0.83	1.45	0.52

apparently somewhat rare. In Indiana, for example, it is known from only seven sites, four of which are lakes examined during the course of this study all of which possessed plus-heterograde oxygen profiles.

Morphologically *O. agardhii* is very similar to *O. rubescens* and *O. prolifica*, from which it is distinguished only with difficulty (the material collected by the writer was identified by Dr. Francis Drouet). All three forms are reddish-purple in color and differ chiefly in size, *O. agardhii* being intermediate. Apparently all three species are similar ecologically, being associated with water blooms in cold water. Smith (1920) discusses an extensive bloom of *O. prolifica* lasting throughout the summer in several lakes in Austria. Edmondson *et al.* (1956) relate that *O. agardhii* was replaced in Lake Washington by *O. rubescens* as a result of the eutrophication of that lake due to greatly increased inflow of domestic sewage. Interestingly enough, they list *Aphanizomenon flos-aquae* as associated with *O. rubescens* under the more eutrophic conditions instead of with *O. agardhii* with which it occurs in Myers Lake. In this connection it might be mentioned that *O. rubescens* occurs in Kreighbaum Lake, which is in the same chain as Myers Lake but is decidedly more eutrophic than Myers.

Many attempts have been made to explain the vertical distribution of phytoplankton. Talling (1957) explains the stratification of the algae in Lake Victoria by means of different rates of sinking due to variations in densities of individual plankters and varying densities of the water at

different levels. Ruttner (1953), however, feels that it is "seldom possible definitely to ascribe the frequently occurring population maxima of the thermocline to this purely mechanical origin. . ." Findenegg (1943) and Rodhe (1948) discuss at length the combined effect of temperature and light on the vertical distribution and cyclic appearance of plankton algae.

Findenegg (1943) lists the optimum temperature range of *Oscillatoria rubescens* as 5-8° C. Other factors being adequate, the main population of *O. rubescens* would follow the movement of the optimal isotherms during the summer. However, optimal as well as minimal light requirements enter the picture. According to Findenegg's classification, *O. rubescens* is a weak-light form (oligophotic). Throughout the summer it thrives in the deeper waters of the metalimnion. If the lower limit optimum of light intensity lies above the level of optimum temperature, then the algae will occur at the higher level, providing the temperature is within the optimal range of the species involved. If the temperature at the minimum light intensity is too high, the alga will disappear from the lake (as in Keutschacher See: Findenegg 1943).

In Myers Lake, *Oscillatoria agardhii* has an almost identical pattern of vertical and seasonal distribution. In the spring when the entire lake is within the optimum temperature range of the species and is in more or less continual circulation, the alga appears to be rather evenly distributed in the lake. With the warming of the surface, the upper level of the optimum temperature range (estimated to be 6-8° C) descends along with an increasing concentration of *O. agardhii*. The descent of this population is stopped when the lower limit optimum of light intensity is reached at about 9-10 meters. Maximum oxygen production occurred slightly above the level of maximum population density at a light intensity of 1-2% surface illumination, although some assimilation took place at less than 0.5% of the surface illumination.

Rodhe (1948) tried to determine experimentally the specific values for light intensities and temperature as they affected the growth of plankton algae. Light and temperature are related in a very complex, complementary manner. For either factor the level of optimum intensity and the corresponding magnitude of production depends on the intensity of the other factor. Rodhe found experimentally that *Melosira islandica helvetica* reached its maximum growth at a temperature of 5° C and light intensity of 1700 lux. These conditions were approximated most closely in nature during November when the most dense populations of *Melosira* were observed with temperature of 4° and light intensity of 2,000-3,000 lux.

Using much the same procedures as Rodhe, the writer has calculated the average light intensity for Myers Lake at the surface and at selected depths in the metalimnion (Table 11). Light intensities are plotted graphically with temperatures for 1954 in Figure 7. Using Rodhe's terminology certain generalizations about the ecological requirements of *O. agardhii* can be drawn by inspection of these data and Table 10.

The lower light limit optimum for *O. agardhii* seems to be ca 200-300 lux. While the lower temperature limit optimum cannot be determined with certainty, it is probably below 6° C. The upper temperature limit is more difficult to estimate. At no time during the summer was a meas-

TABLE 11. Average light intensity (lux) at surface and at selected depths in the metalimnion on the 15th day of the month (calculated with 6% loss from surface reflection)

Original data from Hutchinson (1957)

interpolated to latitude $41\frac{1}{2}^{\circ}$ N.

Depth m	Month					
	April	May	June	July	Aug.	Sept.
0	46,157	48,898	49,475	49,042	47,239	41,614
6	2,126	2,252	2,279	2,259	2,176	1,917
7	1,085	1,149	1,163	1,152	1,110	978
8	651	689	698	691	666	587
9	260	276	279	277	266	235

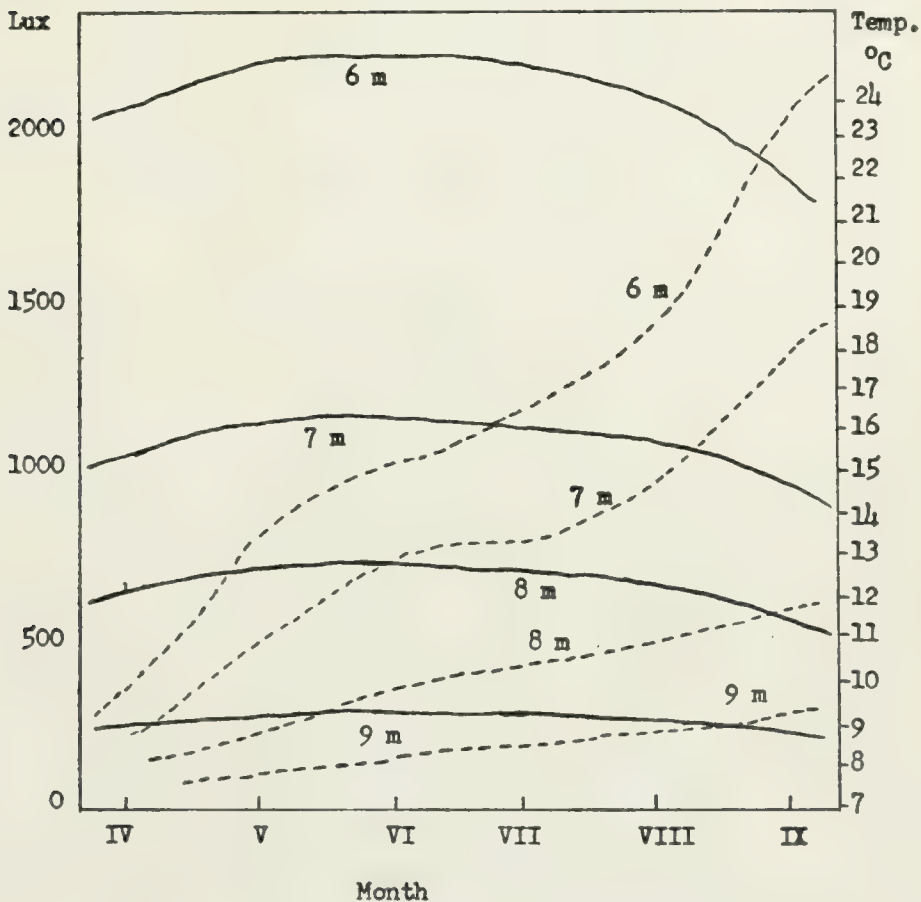


FIG. 7. Average light and temperature in the metalimnion, West Basin.

urable amount of *O. agardhii* observed at a temperature warmer than 18° , and this only in September when light intensities were diminishing. This points again to Rodhe's thesis that the effect of a particular temperature is dependent on the light intensity and duration, and vice versa. During June and July when the days were longest and intensities the highest, no *Oscillatoria* was found above 14° . With shorter days and lower

light intensities of August and September, it was able to survive at as high as 18° . An upper light limit is likewise difficult to ascertain, but it seems certain that *O. agardhii* can endure high intensities (e.g., nearly 46,000 lux at the surface during May) if the temperature is low and the period of illumination is shorter. Rodhe points out that during June and July the actual intensity during midday may be as much as 100% greater than the average for the day, while midday intensity during early spring and late fall will not exceed the average for the day by nearly so large a percentage.

The average intensity of light at the 9-meter level remained fairly constant throughout the summer. But during June when the period of illumination was the longest, the maximum plankton population moved down to the 10-meter level. Here a colder temperature prevailed which was evidently closer to the optimum, and a larger crop developed.

The decline of the *Oscillatoria* after June 29 appears correlated in part with immense numbers of the planktonic ciliate protozoa, *Nassula aurea*, which feeds exclusively on the *Oscillatoria*. The protozoa work on the *Oscillatoria* bloom from below because they prefer a cooler temperature ($3-6^{\circ}$ according to Findenegg) and are obviously adapted to anaerobic or near anaerobic conditions. The grazing of the *Nassula* restricts the alga at times to a rather thin stratum. *Nassula* occurred at times in concentrations as high as 12,816/L (10 m; viii.12.52), and concentrations in excess of 1000/L were not uncommon.

STABILITY OF THE METALIMNION

In order for the small daily net production of oxygen in the metalimnion to reach any sizable accumulation, a relatively stable undisturbed water mass is required. Such stability is the product of various geomorphic, meteorological, and morphometric factors. The generalized formula of Ruttner (1953) gives a rough approximation of the over-all stability of a lake. Based on the mean summer temperatures, the stability of the West Basin of Myers Lake varied from 466.7 to 507.2 g/cm² (Table 12). This is a measure of the amount of work that would be required to render the lake homothermous at the given mean temperature. To be significant on a comparative basis, the stability must be considered in relation to the mean depth (\bar{z}). The stability of Lake Mendota for the first week in August, 1910, was given by Birge (1916) as 514.25 g/cm², but the value of \bar{z} for Mendota is 12.1 m, while for Myers Lake \bar{z} is 6.9 m. Ruttner (1953) cited two examples of 6 and 19 g/cm² but also mentions an extreme case of 3,000 g/cm² (based on a single observation). It is the writer's opinion that for a lake of its size, Myers Lake has a high mean summer stability.

Reference has already been made to the high bank that surrounds the lake on all sides except for a narrow opening at the east end. In addition a dense cover of trees lines both the north and south banks. This protects the lake from most winds except those approaching along the long axis of the lake. As a result of this protection, the metalimnion forms early in the spring at a relatively shallow depth. Unusually strong winds in 1954 resulted in a less stable stratification. The reduced stability is

TABLE 12. Mean summer temperatures, West Basin

Depth m	Year*			
	1952	1953	1954	1955
0	26.60	27.19	27.51	27.00
1			26.67	26.65
2			25.91	26.24
3	25.96	26.73	24.77	25.76
4	24.61	25.20	23.20	22.94
5	20.47	21.19	19.89	19.84
6	15.62	16.14	16.31	15.67
7	12.33	13.25	13.11	11.97
8	10.18	11.74	10.36	9.55
9	8.71	10.56	8.68	8.19
10	7.82	9.73	7.64	7.34
11	7.09	8.99	7.04	6.73
12	6.81	8.69	6.58	6.38
13		8.43	6.43	6.19
14		8.29	6.34	6.10
15	6.50	8.16	6.28	6.01
16		8.03	6.25	5.93
17	(6.40)**	7.90	6.25	5.89
Mean	17.07	18.17	16.83	16.73
Stability (\bar{S}) g/cm ²	487.5	507.2	466.7	487.1

* 1952: June 26-Aug. 28
 1953: June 19-Aug. 24
 1954: June 8-Aug. 10
 1955: June 15-Aug. 23

** Estimated.

also correlated with the lowest mean oxygen maximum observed in the metalimnion during the period covered by this investigation (Table 2).

The stability of each layer, E_z , gives an indication of the protection afforded the underlying layers due to density differences imposed by the thermal gradient during the period of stratification (Table 13). The value of E_z is the amount of work needed to "push" 1 cm³ of water from depth $z-1$ (meters) down to depth z . This is, in effect, another index of thermal resistance to mixing. In 1952 and 1953 there were large values of E_z at 5 and 6 m that prevented much turbulent action from breaking through into the clinolimnion.

It is possible, through the McEwen-Hutchinson method (Hutchinson 1941, 1957), to determine the extent of turbulence by means of temperature changes in the clinolimnion. The clinolimnion is defined as the region below the thermocline, in which the rate of heating decreases approximately exponentially with depth. The clinolimnion includes the lower part of the metalimnion and the upper part of the hypolimnion. Even though there was not a perfect fit all the time, it was thought worth-while to calculate these coefficients for the clinolimnion of Myers Lake based on mean summer temperatures ($A_{\theta z}$, Table 13). The mean values for $A_{\theta z}$ are more significant than the values for individual strata, although the

TABLE 13. Stability E_z ($\text{g}/\text{cm}^4 \times 10^{-6}$) at selected depths
and the clinolimnetic coefficient of eddy conductivity
 $A_{\theta z}$ ($\text{g}\cdot\text{cm}/\text{sec.} \times 10^{-2}$), corrected for molecular
conductivity (0.12×10^{-2})

Based on mean summer temperatures.

Depth m	1952		1953		1954		1955	
	E_z	$A_{\theta z}$	E_z	$A_{\theta z}$	E_z	$A_{\theta z}$	E_z	$A_{\theta z}$
1	0.57		0.42		2.33		0.96	
2	0.57		0.42		2.05		1.11	
3	0.57		0.42		2.71		1.28	
4	3.51		4.08		4.14		7.07	
5	9.63	0.25	9.59	0.16	7.35		6.85	
6	8.97	0.24	9.69	0.16	6.65		7.59	
7	4.56	0.02	4.25	0.11	4.71	0.27	5.05	0.32
8	2.25	0.07	1.82	0.04	3.04	0.46	2.38	0.30
9	1.19	0.04	1.22	0.00	1.37	0.46	1.05	0.24
10	0.57	0.26	0.75	0.04	0.66	0.61	0.37	0.11
11	0.38	0.38	0.59		0.31	0.72	0.29	0.27
12	0.13	0.17	0.22		0.21		0.18	0.28
13								0.18
Mean A_z		0.17		0.09		0.50		0.24

strata where the oxygen maxima occur generally have the lowest coefficients of turbulence.

The coefficients of eddy conductivity for the clinolimnion of Myers Lake are very low. Except for 1954 there was very little more heat transferred through turbulence than through the molecular thermal conductivity of water ($0.12 \times 10^{-2} \text{ g}\cdot\text{cm}/\text{sec}$). Hutchinson (1957) gives values of 0.3 for Lake Quassapaug, 0.21 for Linsley Pond, 0.57 for Sodon Lake, 2.40 for Lake Mendota, and 85.6 for Cultus Lake (all $\times 10^{-2} \text{ g}\cdot\text{cm}/\text{sec}$). One would expect to find higher coefficients of turbulence in larger lakes unless they had a high stable thermocline.

There is also an inverse relationship between the mean value of $A_{\theta z}$ and the mean oxygen maxima (and maximum observed concentration) in the lower part of the metalimnion (Table 2). The highest mean oxygen maximum (19.98 ppm) occurred in 1953 when the coefficient was lowest; the year with the lowest mean oxygen maximum (13.98 ppm) was in 1954 when the coefficient was the highest.

Eddy turbulence extending down into the metalimnion seems to be the only reasonable explanation for the rapid reduction in the oxygen concentrations observed in 1954, *e.g.*, after June 22, July 22, and August 24. Loss of oxygen by diffusion can be discounted (Hutchinson 1957). The highest observed rate of oxygen consumption (respiration) would approximate the net oxygen change in some cases only if total darkness existed during the period. The actual rate of respiration for 8 meters on August 26, 1954, alone would have reduced the oxygen content at that level from 17.0 ppm to 16.4 ppm by August 28, whereas the actual

concentration on the latter date was 13.8 ppm. The three dates just mentioned as being periods of greatest oxygen changes in the metalimnion also follow the dates of the three major windstorms in Marshall County in 1954.

DISCUSSION

There is a strong tendency toward regionalism in lakes that show metalimnetic oxygen maxima. In the Twin Lakes Chain, of which Myers is a part, Cook Lake showed a maximum of 13.7 ppm O_2 at 6 m (vii.20.53), Lawrence Lake, 11.3 ppm at 6 m (vii.17.53), and Hollem Lake, 8.6 ppm at 5 m (vii.20.53). Kreighbaum Lake and Mill Pond showed normal clinograde oxygen curves.

All of the lakes reported by Birge and Juday (1911) as having metalimnetic O_2 maxima belong to the Waupaca chain of lakes. Many of the Japanese lakes with similar oxygen maxima likewise are located in closely associated groups or chains (Yoshimura 1938).

Lakes of a closely related chain are likely to possess similar morphometry and to have similar concentrations of dissolved nutrients. Such data for lakes with metalimnetic oxygen maxima are too meager to allow many comparisons with lakes not having such maxima, but some preliminary generalizations might be made.

The production of a true metalimnetic oxygen maximum as defined earlier is due to the complex interrelation of three factors.

The first of these is transparency. Light transmission in lakes of low color and negligible tripton is affected mostly by concentrations of plankton. Plankton production per unit volume at a given depth is controlled largely by the concentration of dissolved nutrients. The depth of light penetration is inversely related to concentrations of plankton in a given water column. Hence, transmission of light into the metalimnion is likely to be correlated with low epilimnial productivity due to minimal concentrations of nutrients in the epilimnion.

Since the minerals used by the phytoplankton in the epilimnion can be supplemented only from outside sources during summer stratification, it follows that the fertility of the epilimnion is controlled largely by the amount of allochthonous material entering the surface of the lake. It seems to be characteristic that most of the lakes with deep metalimnetic oxygen maxima are chiefly seepage lakes with a minimum of surface drainage from a very small waterhead.

The second important factor is the depth of the thermocline and its thermal gradient. A high thermocline develops if the lake is well protected by trees and high banks and/or when warm, calm weather occurs early in the spring. The higher the thermocline the greater the thickness of the photogenic zone in the clinolimnion. Since the fetch plays a dominant role in determining the intensity of wave action, high thermoclines are more likely to occur in small lakes. In the lakes studied so far there is in general a direct relation between size (area) of the lake and the depth of the oxygen maxima, the latter occurring higher in the smaller lakes. The relation of size to depth is expressed by the parameter $\text{max. depth (m)} / \sqrt{\text{area (ha)}}$ which ranges from 2.91 to 6.96 for the lakes with metalimnetic oxygen maxima.

Sometimes a very small, well protected lake will develop such an extremely high and intense thermocline that a large part of the trophogenic zone lies below the thermocline. Such a condition, which is usually somewhat temporary, often produces large oxygen maxima just below the surface. Wyland Lake, a small (3.3 ha) lake in Kosciusko County, Indiana, developed an oxygen maximum of this sort during 1955 (Fig. 8). On June 28, 1955, the value of E_z between the surface and 1 m was

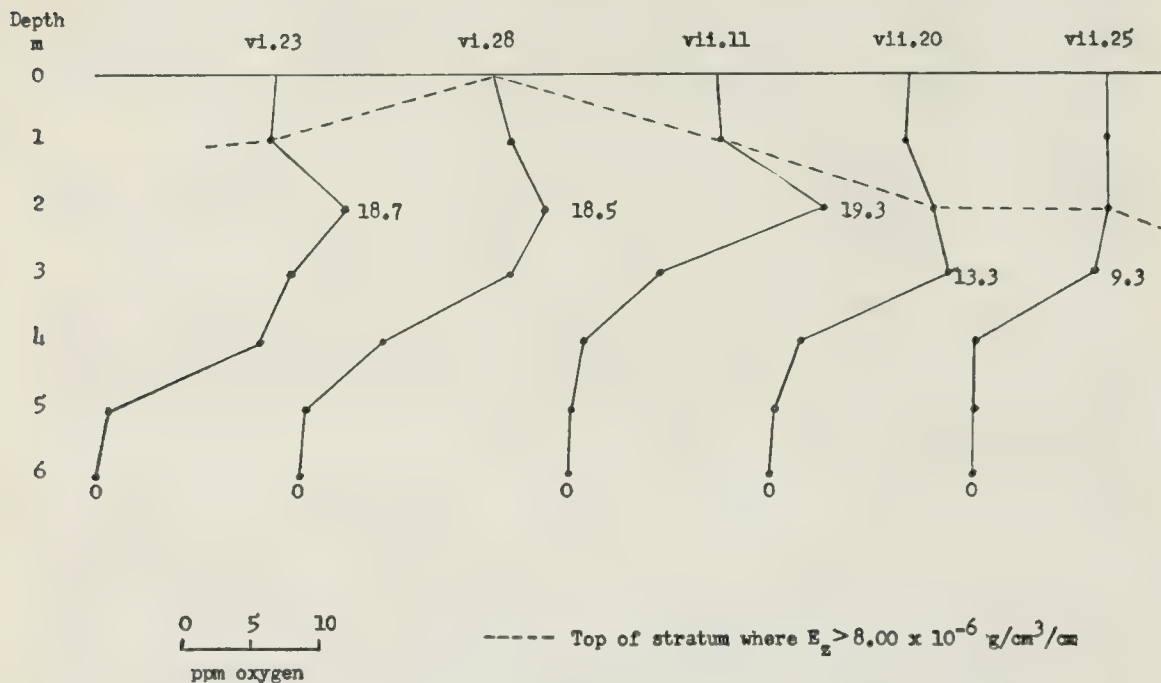


FIG. 8. Oxygen distribution in Wyland Lake during the summer of 1955.

$9.77 \times 10^{-6} \text{ g/cm}^3/\text{cm}$. As the thermocline dropped later in July the very productive layer at 2 m became a part of the epilimnion, and the oxygen maximum disappeared.

The stability of a lake reflects the intensity of thermal stratification and hence the degree to which the lake will be influenced by surface winds. More stable lakes are likely to have high stability/mean depth ratios. For the West Basin of Myers Lake $S/\text{md} = 70.8$, while the same index for the East Basin is 47.2. The less stable stratification of the East Basin of Myers Lake is explained on the basis of lower values of E_z at the thermocline which permit more turbulence to enter the lower part of the metalimnion (Table 14).

Morphometry plays a major role in determining the intensity of stratification. One of the most characteristic morphometric indices is volume development. All the pertinent Wisconsin lakes as well as Myers Lake (West Basin) have volume developments greater than unity (1.02 - 1.89). More data must be examined before definite conclusions can be drawn, but it seems reasonable to predict that the type of stratification necessary for the development of a persistent metalimnetic maximum can occur only in lakes with a volume development greater than 1.00 and a max. depth/ $\sqrt{\text{area}}$ ratio greater than 3.00.

TABLE 14. East Basin, Myers Lake,
June 15 - Aug. 24, 1955

E_z is the stability in $g/cm^4 \times 10^{-6}$, and $A_{\theta z}$ the
clinolimnetic coefficient of eddy
conductivity in $g \cdot cm/sec. \times 10^{-2}$

Depth m	Mean summer temperature °C	E_z	$A_{\theta z}$
0	27.10	1.35	
1	26.61	2.36	
2	25.73	2.00	
3	24.96	6.76	
4	22.17	7.99	
5	18.34	6.74	
6	14.27	3.67	0.33
7	11.31	1.93	0.44
8	9.20	0.93	0.34
9	7.82	0.36	0.22
10	7.14	0.14	0.38
11	6.84		
Mean	20.29		0.34
Stability (\bar{S}) g/cm^2 175.7			

The third element implicated in the formation of a metalimnetic oxygen maximum is the presence of an alga adapted to the conditions that exist in the region of the clinolimnion. The major environmental factors involved are light intensity, temperature, and concentration of dissolved nutrients. The layer in which the oxygen maximum develops is bounded at the top by the thermocline and at the bottom by the depth of penetration of minimal light intensity for photosynthesis.

Bluegreen algae, chiefly the Oscillatoriales, seem to be best adapted to the minimal conditions existing in lakes showing a deep metalimnetic maximum, while diatoms are often involved in shallower maxima. Green algae are involved only rarely and then only in temporary maxima under a very high thermocline.

Oscillatoria agardhii is known to be the chief phytoplankter in the metalimnion of Myers, Lawrence, Cook, and McClish Lakes. McClish Lake in Steuben County (Indiana) has had known maxima as high as 19.8 ppm at 5 m in the metalimnion. The general chemistry of McClish Lake is similar to that of Myers Lake.

In summary, metalimnetic oxygen maxima, *prima facie*, will occur if the following are present:

1. Water of low color, negligible tripton, and low plankton density in epilimnion.

2. Stable thermal stratification induced by protective surroundings of the lake, moderate wind action, moderate to short fetch relative to depth ($\text{max. depth}/\sqrt{\text{area}} > 3.00$?), and/or a basin with a volume development greater than unity.

3. An alga that finds its optimal range in the conditions existing in the metalimnion.

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APPENDIX

TABLE A. Dissolved oxygen (ppm) and
transparency, West Basin (Station B)1952

Depth m	June 26	July				August				Sept. 11
		7	15	23	28	5	12	20	28	
0	7.5	7.4	7.2	6.7	7.3	7.1	7.9	7.5	8.2	8.7
1										
2										
3	7.2	7.0	7.4	6.1	6.9	7.0	5.8	7.4	7.8	8.6
4	7.5	5.5	6.7	5.3	6.1	6.9	7.9	6.9	7.3	7.9
5	10.5	9.4	10.9	8.4	8.0	8.5	7.0	6.9	7.2	7.9
6	13.9	11.2	13.5	13.1	12.2	13.7	10.6	9.0	10.3	8.5
7	17.0	14.9	15.8	15.7	13.8	15.5	14.8	15.0	14.3	13.8
8	17.1	18.5	18.5	20.2	19.8	15.7	16.4	18.3	21.9	18.3
9	11.7	17.3	17.0	18.0	16.9	16.7	14.4	8.3	19.2	13.0
9.5	4.7	16.7	15.8	13.9	13.1	12.2	12.4	2.4	11.7	6.3
10	0.8	8.5	2.1	7.9	8.7	0.2	0.9	1.8	3.9	0.2
11	0.5	3.1	0.3	1.7	0.9	0.0	0.0	0.1	0.2	0.0
12	0.0	0.2	0.1	0.0	0.0			0.0	0.0	
13										
14										
15			0.0							
Disc (m)	4.6	5.0	5.2	5.8	3.5	6.0	3.5	5.5	5.5	5.8

TABLE B. Dissolved oxygen (ppm) and
transparency, West Basin1953

Depth m	Station B				Station A					
	May	June			July			August		Sept.
	2	19	25	3	3	14	31	10	24	7
0	10.7	8.4	8.2	7.1	7.4	8.2	8.5	9.7	8.1	7.6
1										
2										
3	10.7	7.8	8.0	7.3		8.1	8.3		8.4	7.7
4		7.7	8.1	8.7	7.5	7.7	7.7		7.4	7.3
5	10.4	7.8	10.1	11.9		9.8	10.3		7.8	7.9
6		13.0	12.3	12.2		12.3	14.9	16.1	12.2	12.1
7	10.5	14.7	14.2	14.4		13.1	16.3	16.7	17.4	19.8
8	10.3	17.6	17.1	17.5	16.8	18.0	21.1	22.1	21.4	23.3
9	10.1	18.6	16.5	17.3	21.1	20.7	18.3	21.2	18.0	12.5
10	10.0	8.4	2.7	1.9	10.7	9.2	2.2	3.0	3.1	0.9
11		5.7	0.0	1.4		1.4	0.2	0.0	0.4	0.0
12		0.2		0.0	0.4	0.0	0.0		0.2	
13	9.2	0.0			0.0				0.0	
Disc (m)		4.7	5.1	4.0	4.3	5.0	4.8	4.3	4.2	4.5

TABLE C. Dissolved oxygen (ppm) and transparency, West Basin (Station A)

1954

Depth m	April		May 15	June					July				
	19	30		8	11	15	22	29	6	13	20	22	26
0	10.5	9.2	10.5	11.5	11.3	10.1	10.4	9.1	8.6	9.7	8.9	8.5	9.0
1													
2	10.5	9.2	10.3	11.5		12.1	11.2	9.0	8.7	9.5	8.9		8.7
3											7.7		8.7
4	10.4	8.8	10.4	10.7	11.4	11.2	13.9	12.0	11.8	8.7	10.2	8.2	7.8
5		11.1	10.4	10.6		12.5	13.6	11.8	11.5	11.5	11.9		11.2
6	11.8	12.2	10.6	11.7	12.6	13.0	14.4	11.9	11.5	11.5	11.6		11.0
7		12.3	10.5	12.5		13.2	15.0	12.2	11.9	11.7	11.6	11.5	11.1
8	10.8	9.6	11.6	13.7	14.6	14.4	16.1	12.9	13.0	13.7	13.2	13.0	12.4
9	10.1	9.2	10.5	12.8		14.9	16.1	13.9	13.3	14.1	14.2	15.6	9.7
10	9.6	8.8	7.7	9.0	9.7	12.9	10.4	11.3	7.6	3.9	3.1	6.7	2.0
11				5.0		4.2	3.0	4.0	3.0	1.2	0.9		0.9
12	9.6	8.5	6.6	3.6	3.8	2.4	1.9	1.3	1.1	0.9	0.7		0.6
13													
14						1.1	1.0	0.8	0.9	0.8	0.6		0.4
15													
16		6.1	5.1	0.5		1.0	0.5	0.5	0.6	0.5	0.2	0.0	0.0
Disc (m)		2.5	4.2	5.9	6.1	5.3	4.1	3.6	4.0	4.2	3.8	3.4	3.6

Depth m	August							September		Oct. 9	Nov. 28
	2	10	20	24	26	28	30	2	4		
0	7.5	8.1	8.4	8.6	8.6	8.1	8.1	7.8	8.0	8.2	7.6
1											
2	7.5	8.2	8.4	8.6	8.3	8.2	8.1	7.9	8.0	8.1	7.4
3	8.0	8.4									
4	7.2	8.4	7.3	7.4	7.9	6.9	6.5	6.9	8.0	7.7	7.2
5	10.5	10.1	6.9	8.6	7.7	7.6	8.2	7.5	8.4	7.6	
6	10.8	11.4	9.7	10.4	11.3	11.4	11.3	11.4	11.6	7.6	7.2
7	11.3	11.7	11.9							7.3	
8	12.5	14.0	15.3	14.2	17.0	13.8	15.5	15.0	15.0	11.1	7.1
9	12.8	11.0	14.6	13.3	13.5	14.4	14.0	13.9	14.3	9.6	
10	8.2	4.7	2.9	5.0	2.7	8.9	2.9	1.7	2.3	2.3	7.2
11	1.4	0.6								0.6	
12	0.4	1.2	0.2	0.5	0.0	0.0	0.5	0.2	0.0	0.5	
13										0.3	
14	0.2	1.0	0.0	0.0			0.0	0.0		0.0	
15											
16	0.0	0.6									
17											7.6
Disc (m)				4.2	4.1	4.0	4.2	5.0	3.2		

TABLE D. Dissolved oxygen (ppm) and transparency, West Basin (Station A)

1955

Depth m	Jan. 31	Apr. 8	May 15	June			July		August	
				15	24	29	13	26	6	23
0	8.4	12.0	9.4	9.8	9.8	9.5	7.9	7.3	6.1	7.5
1		12.0								
2	11.7	11.9	9.4		9.9	9.5	8.0			
3		12.0		10.0			8.0	7.1	6.0	7.5
4	11.9	11.9	10.2		11.3	11.2	10.6	10.0	8.3	7.2
5			11.5		10.6	11.8	11.4	10.7	11.3	11.1
6	11.8	12.0	13.3	12.1	12.5	13.0	15.5	13.6	12.5	12.6
7			15.9	16.3	16.8	16.5	16.5	14.0	15.5	15.2
8	11.4	11.8	15.1	16.3	16.7	15.5	16.8	15.3	13.4	12.7
9			9.7	11.5	6.4	6.7	11.1	1.7	2.2	6.3
10	11.3	11.2	7.5	4.0	1.1	1.6	1.8	0.3	1.4	2.1
11			6.7		0.8	1.3				1.9
12		11.3	6.1	0.8	0.8	1.3	1.0	0.0	0.4	1.3
13										0.6
14			5.4	0.5	0.3	0.6	0.3			0.0
15									0.0	
16					0.0	0.0	0.0			
17	11.4	11.1	1.1	0.0						
Disc (m)		1.2	3.7	4.1	3.4	4.4	4.9			

TABLE E. Temperature ($^{\circ}\text{C}$)West Basin (Station B)1952

Depth m	June 26	July				August				Sept. 11
		7	15	23	28	5	12	20	28	
0	27.6	28.4	26.6	28.5	27.8	25.6	24.4	24.8	26.4	23.5
3	25.4	27.5	26.6	27.8	27.4	25.6	24.4	24.7	24.3	22.2
4	23.2	23.8	24.5	25.2	26.6	25.5	24.3	24.5	23.9	22.1
5	18.0	17.6	19.6	19.0	21.7	21.6	22.4	22.6	22.4	21.7
6	14.0	14.4	15.2	14.6	15.8	15.6	16.0	17.9	17.4	19.7
7	11.9	11.1	11.7	11.4	12.5	12.1	12.8	13.8	14.5	14.6
8	9.8	9.6	9.9	9.8	10.1	10.2	10.3	11.0	11.3	11.0
9	8.5	8.3	8.5	8.4	8.8	9.2	8.8	8.7	9.5	9.5
10	7.5	7.8	7.7	7.6	7.7	7.9	7.9	8.1	8.2	8.3
11	6.8	7.1	7.2	7.0	7.2	7.0	7.1	7.2	7.2	7.4
12	6.7	7.0	6.8	6.6	6.8	7.0	6.8	6.7	6.8	6.9
13								6.6		
14					6.5	6.5				
15			6.7	6.4			6.5		6.5	6.5

TABLE F. Temperature ($^{\circ}\text{C}$)West Basin1953

Depth m	May 2	Station B			Station A					Sept. 7
		June		3	July			Aug. 24		
		19	25		3	14	31			
0	11.7	27.6	26.7	27.0	27.0	26.5	29.1	25.3	24.2	
3	11.5	24.2	26.1	26.8	26.9	26.2	28.7	25.1	23.9	
4		22.8	23.4	23.9	26.4	25.1	26.4	25.0	23.9	
5	11.0	18.7	18.8	19.4	18.8	20.3	22.4	23.8	23.3	
6		14.6	14.6	15.5	14.5	15.6	16.2	18.8	19.4	
7	10.0	12.5	12.2	12.3		13.4	13.2	14.7	15.1	
8	9.5	11.4	11.0	11.1	11.7	11.7	11.6	12.8	12.1	
9	9.3	10.5	9.9	10.2	10.6	10.5	10.4	11.4	11.0	
10	9.1	9.6	9.2	9.2	10.0	10.0	9.4	10.4	9.6	
11		9.4	8.7	8.8	9.2	9.2	8.7	9.3	9.1	
12		9.0	8.5	8.7	9.0	9.1	8.2	9.0	9.0	
13	8.6			8.5		8.6	8.0	8.8		
14		8.4				8.5	7.9	8.5		
15			8.2		8.2	8.4	7.8	8.4		
16						8.3	7.6	8.3		
17							7.4	8.0	7.8	

TABLE G. Temperature (°C)West Basin (Station A)1954

Depth m	<u>April</u>		<u>May</u> 15	<u>June</u>					<u>July</u>	
	19	30		8	11	15	22	29	6	13
0	14.0	17.5	16.6	22.2	26.1	27.4	28.1	28.3	26.8	27.4
1				20.2	25.0	27.0	27.8	27.1	26.6	26.9
2	13.4	17.0	15.5	19.5	21.0	24.1	27.0	26.9	26.4	25.9
3				19.0	19.7	21.0	24.4	25.3	26.4	25.2
4	12.8	15.7	15.0	18.3	19.0	19.5	20.4	22.3	23.2	24.4
5		12.8	14.5	17.9	17.6	17.7	18.5	18.9	19.9	19.4
6	9.8	10.7	13.5	14.6	14.8	15.3	15.6	15.8	16.0	16.2
7				11.2	12.4	12.8	12.0	12.6	12.6	13.3
8				8.6	9.4	9.8	9.8	9.9	10.4	10.3
9				7.6	8.0	8.4	7.8	8.4	8.7	8.4
10				6.9	7.0	7.4	7.0	7.6	7.6	7.4
11				6.4	6.7	6.8	6.7	6.9	6.9	7.0
12				6.1	6.4	6.4	6.4	6.5	6.4	6.6
13				6.1	6.2	6.3	6.3	6.4	6.4	6.4
14				6.1	6.2	6.3	6.3	6.2	6.3	6.3
15				6.1	6.2	6.2	6.2	6.2	6.2	6.2
16				6.1	6.2	6.2	6.2	6.2	6.2	6.2
17				6.1		6.2	6.2	6.2	6.2	6.2

Depth m	<u>July</u>			<u>August</u>			<u>Sept.</u> 4	<u>Oct.</u> 9	<u>Nov.</u> 28
	20	22	26	2	10	30			
0	27.7	27.3	27.0	27.0	25.5	26.8	24.6	17.9	6.8
1	27.4	27.3	26.8	27.0	25.3			17.6	
2	26.9	27.2	26.8	27.0	25.3		24.6	17.3	6.8
3	26.4	26.9	26.5	27.0	24.8				
4	24.5	26.5	25.7	26.1	24.4	25.2	24.4	17.1	6.8
5	21.0	21.0	21.0	22.0	22.2	23.8	24.2	17.1	
6	16.8	16.3	17.2	17.1	18.4	20.5	22.6	16.9	6.8
7	13.2	13.4	14.2	13.8	14.6			16.7	
8	11.0	10.4	11.1	11.2	10.8			12.9	6.8
9	9.1	9.2	9.1	9.7	9.0			10.7	
10	8.0	8.2	7.7	8.4	8.0			8.6	6.7
11	7.2	7.4	7.3	7.5	7.3			7.5	
12	6.7	6.9	6.7	6.9	6.8			7.0	6.7
13	6.5	6.6	6.6	6.6	6.6				
14	6.4	6.4	6.4	6.6	6.6				
15	6.3	6.3	6.4	6.5	6.4				
16	6.3	6.3	6.3	6.4	6.4				
17	6.3	6.3	6.3	6.4	6.4				6.4

TABLE H. Temperature (°C)West Basin (Station A)1955

Depth m	Jan. 31	Apr. 8	May 8	June				July		August			Sept. 1
				15	22	24	29	13	26	6	23	29	
0	2.4	7.1	17.9	20.2	24.0	23.8	24.6	27.1	29.0	30.5	26.7	26.7	24.3
1		7.0	17.6	18.5	23.0	23.7	24.5	27.0	28.3		26.7	26.4	24.3
2	2.7	6.9	17.5	18.2	20.4	23.5	23.9	26.8	28.1		26.5	26.4	24.2
3		6.9	17.5	18.0	19.9	21.0	22.9	26.8	27.5	29.8	26.4	26.3	24.1
4	2.8	6.9	16.2	17.9	19.1	19.7	20.2	22.3	24.3	25.2	26.2	25.8	24.1
5		6.9	14.0	17.3	17.5	18.3	18.4	19.0	20.1	21.0	23.1	24.0	23.8
6	2.9	6.8	10.0	14.2	14.8	13.2	14.3	15.2	15.9	16.6	17.6	17.4	19.4
7		6.7	8.5	9.9	11.0	10.7	11.0	12.2	11.9	13.0	12.9	13.4	13.4
8	3.0	6.6	7.6	8.5	9.0	8.6	8.7	9.5	9.4	10.3	10.6	10.9	11.0
9		5.9	6.7	7.6	7.6	7.5	7.6	8.2	7.9	8.6	9.2	8.9	9.4
10	3.1	5.8	6.4	7.1	7.1	7.1	7.0	7.4	7.2	7.4	8.0	7.6	8.1
11			6.2	6.5	6.5	6.5	6.4	6.8	6.8		7.0	7.0	7.2
12	3.2	5.8	6.0	6.2	6.2	6.2	6.2	6.4	6.4	6.5	6.6	6.6	6.8
13			5.9	6.1	6.1	6.1		6.2	6.2		6.3	6.3	6.3
14	3.4	5.7	5.8	6.0	6.0	6.0					6.2	6.2	6.2
15				5.9	5.9	5.9	5.9	6.0		6.1	6.1	6.2	6.2
16											6.0	6.0	6.0
17	4.0	5.5	5.7	5.8	5.8	5.8	5.8	5.9	5.9		6.0	6.0	6.0

TABLE I. East Basin, Myers Lakea. Temperature (°C)

Depth m	July 22 1954	1955						
		June				July		Aug. 24
		15	22	24	29	13	21	
0	27.2	23.3	24.6	24.3	24.7	27.9	29.8	26.6
1	27.1	19.6	24.6	24.3	24.5	26.9	28.3	26.0
2	26.9	18.5	24.6	24.0	23.8	26.4	28.1	25.6
3	26.4	18.0	22.0	21.5	22.8	26.0	27.4	25.4
4	24.8	17.5	18.6	19.2	20.0	22.1	23.0	24.8
5	22.2	16.3	16.2	16.1	16.4	17.7	18.0	21.5
6	15.6	11.8	12.3	12.2	12.6	13.8	14.1	17.1
7	12.8	9.4	9.7	9.9	10.1	11.0	11.3	13.4
8	10.4	8.2	8.3	8.3	8.5	8.9	9.3	10.3
9	8.6	7.4	7.4	7.4	7.5	7.7	7.9	8.4
10	7.7	6.7	6.7	6.7	6.9	7.1	7.2	7.5
11	7.4		6.6	6.5	6.6	6.9	6.9	7.1

b. Oxygen (ppm)

Depth m	July 22 1954	June 15 1955	July 21 1955	Aug. 24 1955
0	8.3	9.6	7.8	7.3
1			8.2	
2		9.8		
3	8.3		6.9	7.3
4	8.7	10.2	8.1	6.6
5	8.5	10.9	11.1	11.6
6	8.2	12.6	12.5	4.7
7	7.6	3.8	7.2	
8	3.5	0.7	2.2	0.0
9	0.3	0.5	0.4	
10			0.0	
11	0.0			

TABLE J. Light transmission as per cent
of surface illumination present
at each depth in 1955

Depth m	West Basin						East Basin		
	July		August		Sept.	Mean	July		Aug.
	13	26	23	29	1		13	21	24
0	100	100	100	100	100	100	100	100	100
1	54.0	56.2	61.4	70.0	44.8	57.3	54.0	52.0	58.6
2	31.1	33.9	36.8	36.0	30.8	33.7	37.5	35.8	40.1
3	24.9	20.7	24.5	23.3	18.0	22.3	23.3	23.5	27.4
4	15.3	12.5	16.3	16.6	11.8	14.5	14.3	13.8	13.8
5	10.6	7.0	10.2	10.5	8.2	9.3	9.6	8.8	7.3
6	6.0	3.8	4.9	5.3	4.6	4.9	5.2	4.6	3.7
7	2.6	1.8	2.4	3.0	2.9	2.5	2.3	2.4	1.7
8	1.3	0.9	1.5	1.8	1.8	1.5	1.0	1.2	0.5
9	0.4	0.3	0.8	1.0	0.6	0.6	0.08	0.17	0.08
$K_{1\%}$	0.56	0.58	0.53	0.51	0.54	0.54	0.58	0.57	0.62

The Developmental History of the Chironomid and *Chaoborus* Faunas of Myers Lake¹

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ABSTRACT

Chironomid larvae have specific differences in their resistance to low oxygen concentrations. Hence, in stably stratified lakes the species of chironomids living in the profundal zone indicate indirectly the production of the lake. Chironomids and *Chaoborus* larvae have sclerotized parts which are preserved in the sediments. In order to see what variations in production can take place during the development of a lake, the remains of these organisms were sampled from a core 10 m long taken in 17.3 m of water in Myers Lake, Indiana. This lake has severe hypolimnetic oxygen depletion. *Chaoborus punctipennis*, *C. flavicans*, and *Chironomus* spp. dominate the profundal benthos at present. The sediments are highly calcareous, and low in organic matter.

Sergentia coracina heads were present in all samples from the lowermost sample (27.39 m) to 21.84 m, and in none of the samples above this level. These heads were identified to species by means of both morphological and ecological characteristics. This species can withstand moderately low oxygen levels. Polyoxybiont forms such as *Tanytarsus* were never abundant. In two samples from a core taken in 8.3 m of water *Tanytarsus* heads were much more abundant. Hence, the few *Tanytarsus* heads in the profundal core were probably redeposited from the littoral zone.

Samples of the profundal benthos were taken from 16 northern Indiana lakes. In three of these—James, Crooked, and Oliver Lakes—*Sergentia coracina* larvae were found. These lakes have more oxygen remaining in the hypolimnion than the others. The other lakes had *Chaoborus* larvae and usually *Chironomus* larvae. Most lakes had *C. punctipennis*, and in 5 of them, including Myers Lake, *C. flavicans* was also present. *C. albatus* was found in two of the lakes. One sample from the lower sediments of Tippecanoe Lake had numerous *Sergentia* heads. Thus, *Sergentia* is living now in 3 of these lakes, and did live in at least two of them.

Chaoborus punctipennis mandibles were scarce or absent in the lower sediments of Myers Lake; they became more abundant later, but before *Sergentia* disappeared. *C. flavicans* came in later still; however, it is only 1/10th as abundant as *C. punctipennis* at present, so that it may have entered the lake earlier than the samples show.

The validity of the sampling technique was examined critically. It seemed adequate for the chironomids, but rather poor for *Chaoborus*. Two marked fluctuations in the number of *Sergentia* heads occurred, which can hardly be due to sampling error. They were caused either by variations in the rate of sedimentation, or in the productivity of *Sergentia*. The latter is believed most probable. A curious and inexplicable positive relationship existed between the numbers of *Plumatella* statoblasts and *Sergentia* heads.

These data indicate that Myers Lake had moderately severe oxygen depletion initially, and that oxygen depletion gradually and steadily became more severe. Reduction in the volume of the hypolimnion is the most reasonable explanation for this phenomenon. Therefore it is suggested that the productivity of Myers Lake has not varied appreciably during its developmental history.

INTRODUCTION

The macrobenthos of the profundal zone of ~~eutrophic~~ lakes typically consists of just four major components: chironomid larvae, *Chaoborus*

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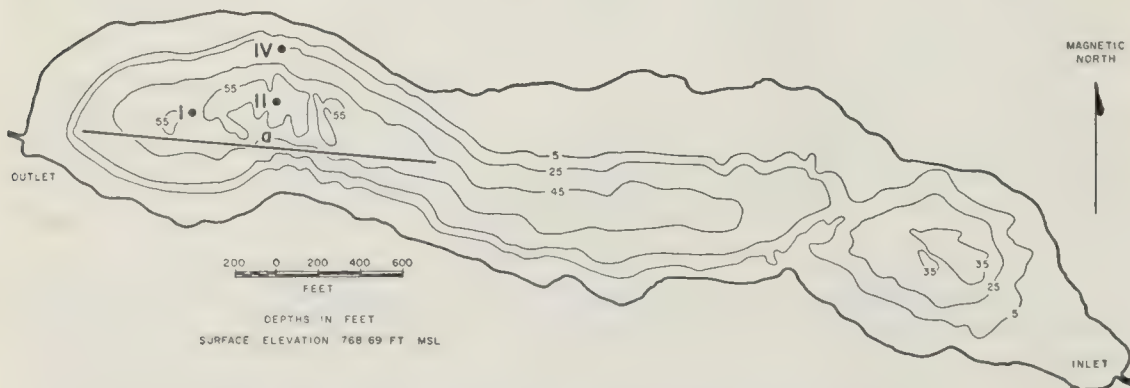
larvae, oligochaetes, and *Pisidium*. One or more of these components may be absent or present in only small numbers, but rarely will other organisms form an important component of the profundal benthos.

Chironomids have been used extensively in Europe for the classification of lakes. Variations in resistance to low oxygen concentrations among various species of chironomids form the basis of this classification. In a stably stratified lake, the amount of oxygen remaining in the hypolimnion at the end of summer stagnation will be a function of the amount of production in the trophogenic zone, provided the volume of the hypolimnion and the duration of stratification are constant. Thus the species of chironomids present indirectly indicate the general level of production in a lake. This was recognized by Thienemann in the early years of this century, when he classified eutrophic and oligotrophic lakes as *Chironomus* and *Tanytarsus* lakes, respectively. Since then, this classification has been refined considerably, especially by Brundin (1949) in his study of the oligotrophic lakes of southern Sweden. This general approach to the study of production is believed to be valid (cf. Brundin 1956), although it is not without shortcomings. These will be dealt with in the Discussion.

Chironomid larvae and *Chaoborus* larvae have hard parts, which are preserved in the sediments. If these remains can be sampled adequately and identified accurately, the possibility exists of reconstructing the past populations of chironomids and *Chaoborus* and of determining the changes in general level of production that have taken place during a lake's development.

METHODS

A Livingstone piston sampler (Livingstone 1955b) was used to obtain cores of the sediments. This sampler took monoliths 3.7 cm in diameter and 1 m in length. A casing pipe was used in several instances to prevent the extension rods from bending excessively. The core on which most of the analyses were performed was core M-I. This was taken in June 1956 in 17.3 m of water near the deepest part of Myers Lake (cf. Map 1). In January 1958 three other cores were obtained from Myers Lake. Core



MAP 1. Bathymetric map of Myers Lake. Sites of cores M-I, M-II, and M-IV shown. Line "a" represents radius of hypolimnion chosen for the calculation of the volume of the hypolimnion. (Adapted from map prepared by the U. S. Geological Survey and the Indiana Department of Conservation.)

M-II was also taken in the deepest part of the lake; the water depth at this time and place was 18.57 m. Core M-III was taken only 1.5 m away from M-II. It consisted of only the upper 4 m of sediment, and was taken because the upper 4 m of sediment in core M-II were not satisfactorily sampled. The water depth recorded for core M-III was only 18.30 m, so this casts some doubt on the accuracy of the water depth measured for core M-II. The same day core M-IV was taken in 8.3 m of water. The exact location of cores M-II and M-IV was determined by triangulation with a plane table and alidade. Their locations are shown on Map 1.

Finally, a core 8 m long was obtained from the central basin of Tippecanoe Lake (Kosciusko County) in January of 1957 in 35.10 m of water.

Although rubber stoppers were inserted into the sample tubes as soon as each sample tube was brought up, these stoppers frequently were pushed out as the sediment expanded, so that a few cm of sediment were lost from the bottom of the monoliths in most cases. This accounts for the fact that almost all the monoliths obtained were less than 1 m in length (cf. gross stratigraphy of core M-I). The monoliths were stored in the sample tubes in a 5°C room. They were eventually extruded into aluminum half shells. The standard procedure adopted was to wrap each extruded core in Saranwrap, cover with another half shell, and then wrap the whole in wax paper, which was folded over at the ends and held snugly with rubber bands. This arrangement reduced water loss to a minimum. Before this standard procedure was adopted the treatment of the cores varied, and parts of some of them dried out considerably. Cores M-II, M-III, and M-IV were kept in a deep freeze (temperature about -35°C) overnight, and extruded the next day. The extrusion of the frozen monoliths worked very well, but it was found that numerous splits developed in the sediment when the monoliths thawed. Thus freezing the monoliths is not recommended.

Samples of 1 ml and 0.2 ml of wet sediment for midge analysis and chemical analysis, respectively, were measured in short glass cylinders. These samples were taken at intervals of 10 cm to 1 m. Deevey (1955a, p. 294) gives an excellent discussion of the relative merits of this method versus the method using displacement of water.

For the midge analysis each sample was extruded into an evaporating dish to which 15 ml of 10% KOH was added. The sample was then boiled for several minutes to a half-hour. During this time it was placed on a magnetic stirrer a couple of times for a few minutes. After boiling and stirring the sample was diluted and then strained through a sieve with apertures 0.125 mm wide (U. S. Standard Sieve Series No. ~~100~~ 120). Sieving was the only way in which the volume of sediment necessary for midge analysis could be reduced to manageable proportions. The fine sediments were rinsed through the sieve with a fine jet of water from a hypodermic syringe fitted with a 19-gauge needle. The sieve was then inverted over a large beaker and the residue rinsed off the sieve with the syringe. Great care was taken to prevent any of the sample from dripping off when the sieve was turned over.

This diluted residue was allowed to stand for at least a half-hour, usually overnight. Then the supernatant was decanted back through the

0.125 mm sieve. The residue remaining in the beaker was treated with several ml of 10% HCl. Then what little residue was retained from the supernatant was rinsed back into the beaker. The suspension in the beaker, the volume of which was now considerably reduced, was then decanted into two 15 ml centrifuge tubes and centrifuged. The supernatant was decanted into a small scored petri dish and examined at 15x under a dissecting microscope for any midge remains that had not centrifuged out. At any time that there was doubt as to the identity of a fragment it was examined at 45x.

The residue was examined at 45x under a dissecting microscope, a small portion at a time, on a scored microscope slide. All remains of chironomids and *Chaoborus* were picked out with a minuten Nadel glued to the end of a matchstick and placed in a drop of water on another microscope slide. The few arachnids and ceratopogonid heads seen were also removed, and in some samples all bryozoan statoblasts and cladocera ephippia were picked out. Any unusual microfossils were also removed. This procedure was very time-consuming, but no better method was devised.

The remains recovered were then mounted in polyvinyl lactophenol. A systematic examination of the entire slide was made at 80x on a compound microscope fitted with a graduated mechanical stage. The location of all fossils was noted by the stage coordinates. Thus it was possible to refer back to any individual specimen.

Samples for chemical analysis were extruded into weighed crucibles. All weighing was done on a chainomatic balance on which weights could be estimated to 0.1 mg. Measurements of the water content, carbonate content, and loss on ignition after removal of the carbonate (considered to represent organic matter) were made. Each sample was dried in an oven at a constant temperature of 80°C for 12 hours, following the recommendation of Züllig (1956). After cooling the sample in a desiccator it was reweighed. The loss in weight represents the amount of water. Then the sample was transferred to a large evaporating dish, and 10 ml of concentrated HCl were added, again following Züllig's procedure. The sample was allowed to stand for 24 hours, then was diluted with distilled water and filtered with suction through a weighed disc of filter paper. The residue on the filter paper was rinsed with 20 ml of warm distilled water, put back into the crucible and dried for 12 hours at 80°C. After cooling in a desiccator the sample was again weighed. The loss in weight represents the quantity of carbonate. For most of the analyses Whatman No. 1 filter paper was used. Whatman No. 50 filter paper was used for a few of the later analyses. Since the results from both filter papers are of the same magnitude, it is believed that any error in using the coarser Whatman No. 1 filter paper is not excessive. It would tend to overestimate the amount of carbonate in the samples. Finally, the filter paper and residue were ignited in a muffle furnace for 3 to 5 hours at 300-500°C, cooled, and weighed. The loss in weight represents the organic matter.

Other methods are best considered under the appropriate section.

DESCRIPTION OF MYERS LAKE

Myers Lake is located in Marshall County, about 4 miles southwest of Plymouth, Indiana, in Sec. 24, T. 33 N., R. 1 E., and Sec. 19, T. 33 N., R. 2 E. It lies on calcareous till of the Maxinkuckee moraine, which was deposited in the Cary subage of the Wisconsin. A detailed description of the lake may be found in Eberly (1959). Only the more pertinent features are mentioned here.

The lake has an area of 38.8 ha, and a maximum depth of 18.0 m. A subsurface bar divides the lake into a small and shallow east basin and a larger and deeper west basin. There is a broad and shallow littoral shelf, extending to a depth of about 1 m, which is covered by a rich and varied submersed vegetation (cf. Map 1). A high ridge covered by oak-hickory forest surrounds Myers Lake on all sides. The land tends to slope away from the lake from the top of the ridge. Thus the watershed is very small, and there is a protected "geomorphic setting."

These two characteristics lead to a relatively low level of dissolved minerals and to an unusually stable thermal stratification. A good index of the total dissolved minerals is the specific conductance. This ranged from 190 to 250 mho $\times 10^{-6}$ at 18°C in the trophogenic zone. The water is fairly clear and oligohumic: the mean depth of 1% light transmission in summer is 8.4 m, and the color of the surface water ranges from 12 to 16 ppm. The water is alkaline, with a pH of near 7 in the lower hypolimnion, and as high as 8.7 in the epilimnion. Methyl orange alkalinity ranges from 114 to more than 200 ppm CaCO_3 .

Each summer a pronounced metalimnetic oxygen maximum develops (cf. Eberly 1959). This is caused primarily by *Oscillatoria agardhii* Gom. Although in terms of the quantity of nutrients present the lake is mesotrophic, in terms of primary gross production Myers Lake is distinctly eutrophic. The mean gross production is 1.48 g C/m²/day. In view of this high production it is not surprising that from the middle of June until the middle of October there is virtually no oxygen in the hypolimnion.

GROSS STRATIGRAPHY

It has seemed most appropriate to give a brief description of each monolith of core M-I for three reasons: (1) there are no markedly distinct regions, (2) microlaminae occur somewhat discontinuously throughout the core, and (3) each monolith varies in total length.

The monoliths from 21.30 to 27.77 m were extruded 21 March 1957; the other monoliths were not extruded until 2 September 1957. Color was measured (using the standards of Ridgway 1912) on 26 March 1958. Depths are measured from the surface of the water.

Core M-I

17.30-18.18 m: Porous and moist gyttja; Brownish Olive from 17.30 to 17.53 m, Grayish Olive in remainder of monolith. By 26 March 1958 the sediments had shrunk greatly, and were not nearly so moist as when first extruded.

- 18.30-19.13 m: Microlaminae throughout this monolith; color between Brownish Olive and Olive, although neither of these was a good fit.
- 19.30-20.24 m: Microlaminae from 19.30 to 19.79 m; 19.79-20.10 m without distinct laminae; Buffy Olive from 19.30-19.70 m; between Brownish Olive and Light Brownish Olive from 19.80-19.85 m; Deep Grayish Olive from 20.10-20.24 m.
- 20.30-21.30 m: This monolith is not considered, as there was premature release of the piston.
- 20.80-20.78 m: Microlaminae over entire monolith; Saccardo's Umber to Warm Sepia from 21.48-21.78 m; rest of monolith Grayish Olive.
- 21.30-22.26 m: Microlaminae from 21.30 to about 22.10 m; they become indistinct below this point; colors observed were Citrine Drab and Dresden Brown. At places these colors occurred side by side; the microlaminae were continuous between the two colors in such cases.
- 21.30-22.18 m: This is the "duplicate" monolith, taken from the side rather than the center of the boring platform. Microlaminae over virtually the entire length of this monolith; color not measured.
- 22.30-23.13 m: Microlaminae over most of monolith, except 22.40-22.45 m; color is Light Brownish Olive, with a narrow zone of Bister at 23.28 m.
- 23.30-24.08 m: Microlaminae over entire monolith; gyttja much more clayey than in previous monolith; a gritty layer (gray sand stratum) at 23.63 m; a zone of Saccardo's Umber at 23.78 m.
- 24.30-25.04 m: More or less distinct microlaminae from 24.30-24.90 m; color of most of monolith was Cinnamon Brown; the sediment in the middle of the monolith had a peculiar "skin" with wrinkles or blisters on it.
- 25.30-26.05 m: No laminae; Mars Brown to Bister from 25.30-25.90 m; 25.90-26.05 m Deep Grayish Olive.
- 26.30-26.93 m: The 26.30-26.45 section broken off, dried to rock hardness; fair microlaminae occurred from 26.35-26.61 m; 26.61-26.93 m section broken off also, and dried to rock hardness; upper 20 cm Deep Olive, remainder of monolith Saccardo's Umber; at 26.45 m another gritty zone consisting of pure calcareous sand, 3 cm wide (color about the same as the rest of the monolith; did not seem unduly dry).
- 27.15-27.71 m: All of the sediments had become quite hard by 26 March 1958; a sprinkling of white spots in the lower 17 cm; Cinnamon Brown in middle of core, Deep Olive in remainder.

All of the monoliths had a black center, indicating that the sediment was black before oxidation. In fact, the laminae did not become visible until the sediment had become oxidized. A surface sample of Myers Lake gyttja was compared with Ridgway's color charts and was found to be "Black," *i.e.*, there was no other color intermixed. This is the only Indiana lake sampled in which the sediments were Black. The darkest color from any other lake (of 16 sampled) was Iron Gray.

Samples taken in the lowermost two monoliths had a noticeably higher content of fine sand grains.

Because of lack of time, observations of the gross stratigraphy were made on only three monoliths of core M-II and one monolith of M-III, plus a cursory observation of the 5 monoliths comprising core M-IV.

Core M-II

21.58-22.40 m: Numerous horizontal splits in this monolith; microlaminae present; a zone of small snail and clam shells from about 22.00 to 22.10 m; a fairly large snail shell was seen at 21.76 m.

22.57-23.46 m: There were only 3 splits in this monolith; microlaminae present; oddly, these laminae are at an angle of about 45°.

24.27-24.92 m: Numerous horizontal splits in this monolith from 24.27 to 24.67 m; distinct microlaminae present; a number of hard, black chunks (like bits of coal) were found in the sample taken from this monolith at 24.87 m.

Core M-III

18.30-19.18 m: Numerous horizontal splits in this monolith; no microlaminae. The other monoliths of this core were not examined.

Core M-IV

Since data on the lengths of the individual monoliths are not available at present, the core as a whole will be described. The entire core extended from 8.30 m to 11.96 m. The upper 7 cm of sediment had many rather large clam shells and many small snail shells. The remainder of the core had quite a few small clam shells, and more small snail shells, although not nearly so many as in the upper 7 cm. The lowermost 13 cm of the core were virtually pure sand, which was highly calcareous. The general color of the core was Grayish Olive.

POLLEN ANALYSIS

A pollen analysis of core M-I by D. G. Frey (1959) shows that the Two Creeks Interval is represented between approximately 25 and 26 m. *Picea* and *Abies* drop to almost zero per cent, and *Betula* reaches a maximum at this level, resulting in a pronounced notch in the *Pinus* curve. Both *Picea* and *Abies* again increase above this level. Andersen (1954) and Deevey (1951), however, found an increase in *Picea* during the Two Creeks Interval. In core M-1 *Ulmus* increases and *Equisetum* drops to a minimum at 25.55 m.

The B-1 (Boreal) zone is represented by a sharp *Pinus* peak at 23.35 m. Above this are the deciduous C zones of post-glacial time, with the Altithermal occurring at about 20 m.

Especially significant is the find of the Two Creeks Interval. This would be expected to occur, as Myers Lake lies on glacial drift of Cary subage.

DEVELOPMENTAL HISTORY

Remains of many kinds have been found in the sediments of bogs and lakes (cf. Knülli 1957 and Frey 1958), although the great majority of sediments have been analyzed for their pollen content only. The remains of chironomids and especially of *Chaoborus* have been relatively little studied. Miscellaneous reports of chironomids include those by Gams (1927), Groschopf (1936), Deevey (1937), Scourfield (1943), Andersen (1943), and Brehm *et al.* (1948).

There have been five studies that have dealt with midges in a more thorough manner. These are Andersen (1938), Deevey (1942 and 1955a), Frey (1955a), and Livingstone *et al.* (1958). The only papers to report *Chaoborus* remains are Deevey (1942) and Frey (1955a). Only Deevey examined the *Chaoborus* remains quantitatively.

Gams (1927) had some of his samples from Lunzer Obersee examined for chironomids by A. Thienemann. Numerous heads of the *Eutanytarsus* group were found in the interstadial gyttja I-II. There was a rapid decrease in number of heads from about level IV on, and from level IX on they were almost lacking. They were replaced by chironomids in the strict sense and by ceratopogonids (*Bezzia*, etc.). This was the first use of chironomids to indicate change in lake type with the development of the lake. Unfortunately, this study suffers from certain defects as far as the chironomids are concerned. No quantitative counts were made, and no drawings or other data were published. Moreover, the sediments sampled were in the shallow part of the lake. The deepest coring extended to only 10 m below the present surface of the lake. Although Obersee is apparently stratified, as evidenced by the severe oxygen depletion and lack of any living chironomids below a depth of 1.5 m (Thienemann 1950), it seems to be a limnocrene. Part of the stability of stratification may be from periodic meromixis. The somewhat similar Lunzer Mittersee has been shown to undergo such a condition (Ruttner 1955).

Groschopf (1936) in his study of the pollen in Grosser Plöner See, found a few chironomid head capsules, and was aware of the possibility of using the chironomids to indicate the condition of the lake. However, he found too few heads to be able to use them for this purpose, and they belonged as far as could be determined to commonly occurring forms. Deevey (1937) found just one *Tanytarsus* head from the interglacial sediments of an extinct Tibetan lake. Although he drew no conclusions from this one head, he did comment at some length on the possibilities of using chironomids as indicators of a lake's type. Cores collected from Windermere were examined for animal remains by Scourfield (1943) who simply reported that he found the remains of "*Chironomus*." Andersen (1943) described a new genus and species of midge, *Dryadotanytarsus edentulus*, which was found by him during his 1938 study of the chironomids in the late-glacial sediments of a Danish bog.

Samples taken by von Sarntheim from Schwarzsee near Kitzbühel, Austria, were examined by Brehm (cf. Brehm *et al.* 1948) for chironomid remains. He claims to have identified *Psectrotanypus longicalcar* head capsules. (This is a synonym of *P. trifascipennis* Zett.) Unfortunately, he does not give any drawing of this head capsule. Outline drawings of the labium of various other midges are given, but the paralabials were not shown, so that the labia cannot be identified even to subfamily.

The five more thorough studies of chironomids and *Chaoborus* will be discussed when evaluating the results from Myers Lake.

Qualitative results

The remains of the chironomid and *Chaoborus* larvae in lake sediments can be identified by two means: morphological characteristics and eco-

logical characteristics. Both of these must be used, and even then there will be many instances in which a precise identification is impossible.

Often more can be done with the information available on morphological characteristics than is realized. It is sometimes possible to identify a remain on the basis of a striking and unique feature, even though it may not be possible to run the remain through a key. Palynologists have recognized this, and use such characteristics for the identification of pollen grains. As in pollen analysis a reference collection of chironomid and *Chaoborus* larvae would be useful. Actually, palynologists have no more to identify pollen grains than is available for the identification of midge remains.

Present keys for the identification of chironomids are not arranged in such a way that distinctive characteristics of the head capsules are emphasized. An example of what can be done by rearrangement of key characteristics is given in the key to the genera and groups of Tanytarsinae on p. 64.

1. Nomenclature

A review of the nomenclatorial problems of the "midges" is given in Townes, 1945, p. 10 ff.). *Tendipes* and *Pelopia* (and their derivatives) have priority over *Chironomus* and *Tanypus*, respectively. Although the former pair of names has been used in a considerable amount of literature, it nevertheless is a fact that in the majority of the literature, both past and present, the latter set of names is used. This is particularly true of the literature on larval midges. Hence, *Chironomus* and *Tanypus* are used in this thesis as a matter of convenience.

The usage of *Tanytarsus* has been confused only since 1945 when Townes used this generic name for an entirely different group of chironomids than it had been used for up to that time.

There are two basic subdivisions of the subfamily Chironominae: the tribes Chironomini and Tanytarsini. These subdivisions have been in use since 1874. They are particularly significant in that "*Chironomus*" lakes and "*Tanytarsus*" lakes are virtually synonyms for eutrophic and oligotrophic lakes respectively. A prodigious amount of literature in which these two names and these two concepts are used has accumulated.

For what seems to me (and many others) a very trivial reason, Townes applied the name *Tanytarsus* to a group which belongs to the Chironomini! Although *Chironomus punctipes* had been selected as the genotype in 1910 everyone has used *Chironomus signatus* as the genotype, because *C. punctipes* did not fit the characters of the genus as designated by Kieffer in 1911. Concerning this practice Townes says: "Selection of genotype by elimination is not a procedure that is sanctioned by recognized rules of nomenclature, or by general use, so *Chironomus punctipes* must stand as the genotype of *Tanytarsus*." The absurd thing about this statement is that obviously the selection of genotype by elimination had been accepted by general use in this instance! Most American authors have followed Townes in his usage of *Tanytarsus*, but not one chironomid specialist in any other part of the world has.

Townes' grouping of *Endochironomus*, *Stictochironomus*, *Lenzia*, and *Sergentia* into one genus might well represent the most natural classifica-

tion. If he had applied some other name than *Tanytarsus* to the group it might have been usable.

Johannsen (1937a and 1937b), Goetghebuer (1928), Lenz (1941 and 1957), Townes (1945), and Brundin (1949) have been used for the identification and nomenclature of the chironomids. Cook (1956) has been used for the identification and nomenclature of the *Chaoborus* species.

2. Identification of *Sergentia coracina*

Head capsules of what are believed to be *Sergentia coracina* Zetterstedt³ formed the principal component of the profundal benthos of Myers Lake in its early history (cf. Table 2 and Fig. 54). Much of the interpretation of the developmental history of Myers Lake rests on the accurate identification of these head capsules. Therefore, the reasons for believing these head capsules to be those of *Sergentia coracina* will be given in detail.

The labium is perhaps the most useful single structure for the identification of chironomid head capsules. In *Sergentia* the labium has 16 rather long and pointed teeth; the first laterals are larger than the other teeth (Fig. 2). Three other genera have a similar labium—*Stictochironomus*, *Endochironomus*, and *Lenzia*. The finer differences in the labium of each of these genera will be considered as well as the other characteristics of the head capsule.

The pattern of striations on the paralabial plates of *Sergentia* is characteristic: they gradually become shorter laterad, and then stop about midway in the paralabial plate (Fig. 2). Almost 60% of the *Sergentia* head capsules had at least one mandible attached, so that the character-

Plate I

All figures were drawn with the aid of a microprojector, at high power (440x) unless otherwise stated. Scales shown in microns.

Sergentia coracina

1. Head capsule. Low power. Core M-I. 22.74 m.
2. Labium and paralabial. Core M-I. 22.74 m.
3. Mandible. Core M-I. 22.74 m.
4. Antenna. Core M-I. 22.74 m.
5. Epipharyngeal plate. Core M-I. 27.39 m.

Stictochironomus sp.

6. Labium and paralabial. Richland Creek.
7. Mandible. Richland Creek.

Endochironomus nigricans

8. Labium and paralabial. Wyland Lake.
9. Mandible. Wyland Lake.
10. Epipharyngeal plate. Wyland Lake.

Endochironomus dimorphus

11. Labium and paralabial. Salt Creek.
12. Mandible. Salt Creek.
13. Antenna. Salt Creek.

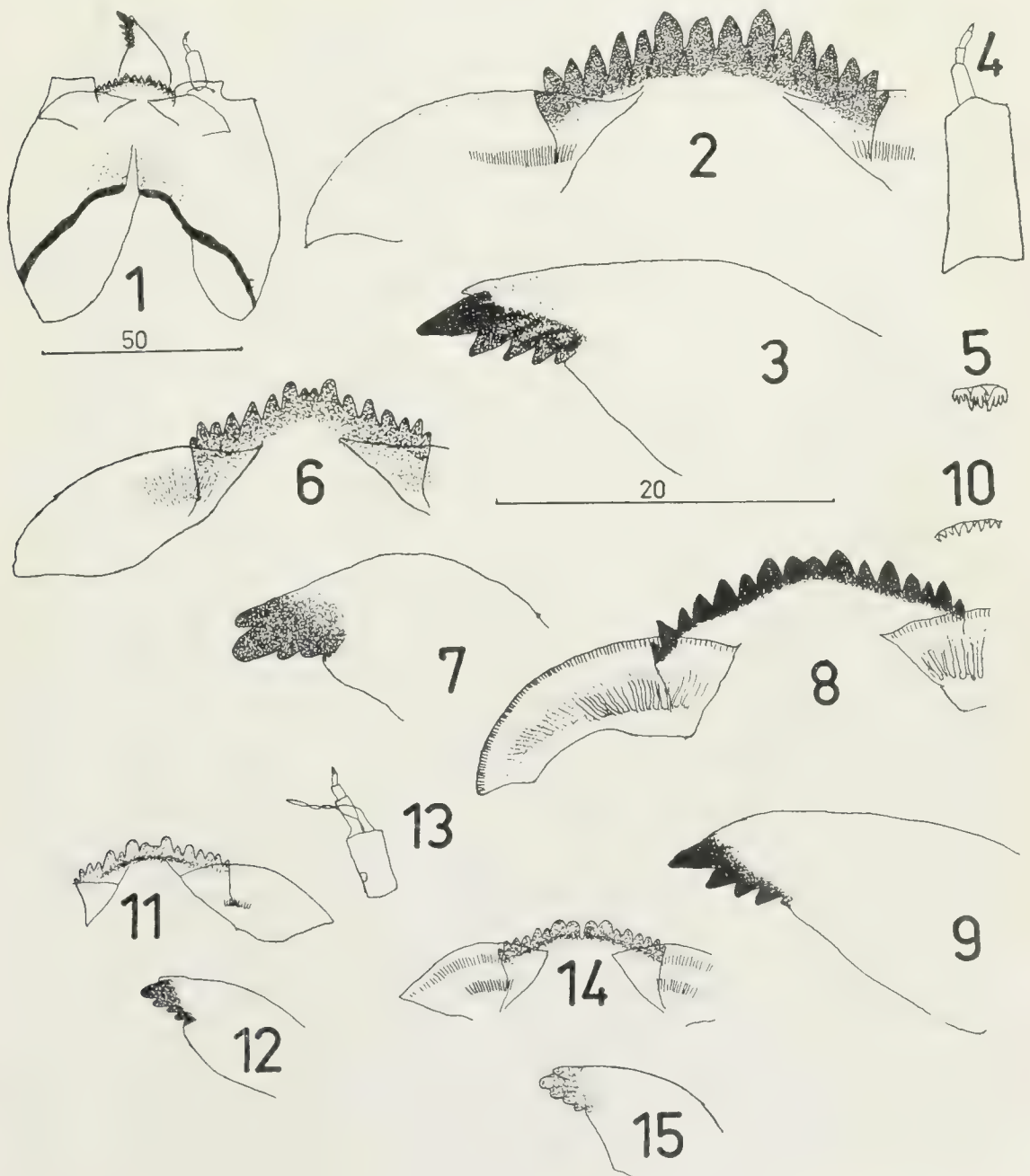
Endochironomus sp.

14. Labium and paralabial. Core M-I. 22.20 m.
15. Mandible. Core M-I. 22.20 m.

³ By the nomenclature of Townes (1945) this would be *Tanytarsus* (*Tanytarsus*) *coracinus*. Miller (1941) called this species *Pentapedilum* (*Sergentia*) *coracinum*.

istics of the mandible are useful in identifying subfossil heads. In *Sergentia* the mandible (Fig. 3) has a dark apex and four dark outer teeth, as well as a pale inner tooth (which is usually more or less hidden by the apex of the mandible). Note particularly that the basal tooth of the mandible is distinctly delimited.

Eight head capsules were found with a complete antenna attached. An antenna can be identified as complete because the terminal segment is conical. In all 8 cases the complete antennae had just 5 segments (Fig. 4). The head shown in Figure 1 was a fourth instar; the antennal ratio (*i.e.*, the ratio of the length of one segment to that of the preceding segment) was $3.7 : 2.5 : 1.0 : 2.7$. This agrees well with the antennal ratio that Lenz (1941) gives for *Sergentia* of $3.5 : 2.0 : 1.25 : 2.0$. The other head capsules with complete antennae were second or third instars,



and their antennal ratios deviated considerably from the ratio given by Lenz. In none of these antennae was it possible to see the ring organ satisfactorily, partly because of detritus attached to the antenna. Nevertheless, it seems strange that the ring organ was not seen more frequently.

A few *Sergentia* heads were found that had the epipharynx attached. The epipharyngeal plate is distinctive, consisting of three hand-like groups of teeth (Fig. 5). The entire head capsule is shown in Figure 1. The darkening at the base of the head on the ventral side is characteristic.

All the features described above check with the description of *Sergentia* given by Lenz (1941). More important, they also agree in every detail with heads of *Sergentia coracina* larvae kindly given me by Lenz. The larvae of all three species of *Sergentia* are apparently identical (Lenz 1941).

No *Stictochironomus* heads were found in the sediments. Larvae of this genus were collected from Richland Creek, in Monroe County, Indiana. The labium, paralabials, and a mandible of one of these heads are shown in Figures 6 and 7. Although the labium is similar to that of *Sergentia*, the teeth are more rounded, and the two median teeth are very small. In many specimens these median teeth are worn down to the base. The striations on the paralabials are very faint. As in *Sergentia*, these striations extend only to the middle of the paralabial plate. However, they do not become shorter laterad. The mandible (Fig. 7) is much different from that of *Sergentia*. Although Lenz (1941, p. 36) states that the mandible has an apex and four outer teeth, this is misleading. It seems to me that the "apex" is really a large and dark inner tooth. Moreover, the basal tooth is hardly visible. Thus the mandible can be described as having a large and dark inner tooth, with a dark apex and two dark outer teeth. These features are shown in Lenz's drawing, and can be seen in Figure 7. *Stictochironomus* is the only one of these four genera with 6-segmented antennae.

Endochironomus is not so easily distinguished from *Sergentia* as is *Stictochironomus*. Indeed, Andersen (1937, p. 31) said that it was almost impossible to distinguish these two genera in the larval stage. However, Lenz (1941, p. 35) stated that the two genera can be separated without any difficulty. Unfortunately Lenz does not explicitly describe the differences between the two genera. Indeed, I have been unable to find any statements in the literature on how these two genera are to be distinguished. On the basis of the descriptions given (Goetghebuer 1928, p. 34; Lenz 1941, pp. 31, 32) one would have to agree with Andersen. Nevertheless, in the drawing in Goetghebuer (1928) and Lenz (1957) it can be seen that the basal tooth of the mandible of *Endochironomus* is not distinct.

The material available for examination included larvae of *Endochironomus nigricans* and *E. dimorphus* from a couple of Indiana lakes and from Salt Creek, Indiana, and of three heads of *Endochironomus* sp. recovered from the Myers Lake sediments. The larvae were identified by Johannsen's (1937b) key. Since the larvae were not reared, identification to species is not positive. The long antennal blade is characteristic of *E. dimorphus* (Fig. 13).

In all three of these species the teeth of the labium were shorter and somewhat more rounded than in *Sergentia* (Figs. 8, 11 and 14). The labium was almost black in *E. nigricans*. Also, in every case the basal tooth of the mandible was not separated from the rest of the mandible (Figs. 9, 12, 15). The striations on the paralabial plates were different in each of the three species examined, and all three differed from *Sergentia*. Those on *E. nigricans* were very strong and thick, especially in the median half of the paralabial (Fig. 8); on *E. dimorphus* they were relatively inconspicuous, and occurred only at the base of the paralabials (Fig. 11); and in the heads from the sediments the striations occurred in two bands (Fig. 14). The epipharyngeal plate of *E. nigricans* (Fig. 10) is markedly different from that of *Sergentia*, as it consists of a bar with several small teeth of varying sizes along it. Lenz (1957) stated that this type of epipharyngeal plate is characteristic of the entire genus.

Lenzia, according to Lenz (1941, p. 30) is virtually identical to *Sergentia*.

In summary, of the four genera that have a labium with 16 teeth, and with the first laterals larger than the rest, *Stictochironomus* can be distinguished easily from the others by the small middle pair of labial teeth and by the large dark inner mandibular tooth, *Endochironomus* can be distinguished from *Sergentia* by the shorter labial teeth, different pattern of striations on the paralabial plates, mandibular teeth, and epipharyngeal plate, but *Lenzia* cannot be distinguished from *Sergentia*, nor can the species of *Sergentia* be separated from one another in the larval stage.

Ecologically *Stictochironomus* and *Sergentia* could not be distinguished, as both genera have species that are part of the *Tanytarsus lugens* community of Brundin. Hence it is fortunate they can safely be distinguished by morphological characters.

Even though *Endochironomus* can be distinguished from *Sergentia* morphologically, a discussion of the ecological requirements of *Endochironomus* is desirable both for comparison with those of *Sergentia* and to clear up some confusion that exists in the literature. *Endochironomus* is generally considered to be an inhabitant of the littoral zone, and absent from the depths of lakes (Lenz 1957). Townes (1938), Lindeman (1942), and Curry (1952) all found *Endochironomus* larvae in the littoral zone. Only Curry found any such larvae in the profundal zone. He reported *E. jucundus* var. *dimorphus* from the 10 to 21.9 m zone of Coldwater Lake, Michigan. Miyadi (1933), Humphries (1936), and Miller (1941) are the only other authors that have reported *Endochironomus* from the profundal zone. Since Miyadi used only the larvae for identification (none was reared) Thienemann (1954, p. 509) has suggested that Miyadi mistook *Sergentia* for *Endochironomus*. It is not clear just how Humphries arrived at the conclusion that *Endochironomus* sp. occurs in the profundal of Windermere. At least it is certain that *Endochironomus* does not occur in large numbers in the profundal of that lake.

Miller (1941) reported that *Endochironomus nigricans* was confined to the profundal zone in Costello Lake, Ontario, Canada, and that *Sergentia coracina* lived both above and below the metalimnion. These anomalous results are explained by the methods Miller used. The distri-

bution of most species of chironomids in the lake was studied by means of emergence traps which floated on the surface of the water. These would not accurately indicate the depth from which the adults came. The distribution of *Endochironomus nigricans* was based on the larvae (p. 36). Although adults of both species were collected, no larvae of either was reared. Since Miller makes no comment about differentiating the larvae of the two species, it seems almost certain that what he called *Endochironomus nigricans* larvae were really *Sergentia coracina* larvae.

Additional support for the unlikeliness of *Endochironomus* larvae living in the profundal zone in any large numbers is provided by two excellent studies of the feeding habits of four species of this genus, including *E. nigricans* (Berg 1950, Walshe 1951). All four species were found to be net-spinning plankton feeders living on or in submerged aquatic plants.

In summary: there are four records of *Endochironomus* larvae in the profundal zone (if all the Japanese lakes with these larvae are counted as one record). The two reports of such larvae being abundant in the profundal zone are almost certainly erroneous; in all likelihood the larvae of *Sergentia coracina* were mistaken for those of *Endochironomus*.

Lenzia larvae are typically littoral forms (Lenz 1941, Thienemann 1954). Only one species, to my knowledge, is a typical profundal dweller. This is *Lenzia patagonica* Brundin, found by Brundin (1956, p. 216) in the profundal zone of lakes in southern Chile, South America. Thus one would not expect head capsules of *Lenzia* to be abundant in the profundal sediments of Myers Lake, or any other Holarctic lake.

There are just three species of *Sergentia*: *S. coracina*, *S. longiventris*, and *S. psiloptera* (Brundin 1949). The last species has only been reported twice—once from Swedish Lapland and once from Bear Island (Brundin 1949, p. 776). *S. longiventris* is more common. It is characteristically found in polyhumic lakes and is an obligatory shallow water form. It is a cold stenotherm. Hence, it is found only in more northern localities, in which the water of the littoral zone never becomes too warm.

Sergentia coracina is by far the most common species. It has been collected in numerous localities in northern Europe, and in the alpine regions of southern Europe. There are a few reports from Canada and the northern United States (Johannsen 1934, Townes 1945). This species is also a cold stenotherm, but it can live in either shallow or deep water. Consequently, it is able to survive in the profundal zone of stably stratified lakes even though the surface waters may become quite warm. It is a member of the *Tanytarsus lugens* community of Brundin (cf. Discussion), which is characteristic of oligotrophic lakes (i.e., with relatively high hypolimnetic oxygen content). However, *Sergentia coracina* can withstand a considerably lower oxygen content than can most of the other species in this community. Consequently, it can survive in lakes in which the other members of the *Tanytarsus lugens* community are absent or reduced in numbers.

From the foregoing discussion of morphological and ecological characteristics of *Sergentia*, *Stictochironomus*, *Endochironomus*, and *Lenzia* it seems that *Sergentia coracina* is the only species to which the head capsules from the early sediments of Myers Lake could belong.

3. Identification of other chironomids

Several other kinds of chironomid head capsules could be identified to genus or group, and some occurred in appreciable numbers. These are discussed in taxonomic units, *viz.*, Chironomini, Tanytarsini, Tanypodinae, and Orthocladiinae.

Chironomini are readily identified by the fan-shaped paralabial plates. *Polypedilum* (*sensu* Townes 1945) has a distinctive labium of 14 teeth, in which the first two laterals are much shorter than the teeth on either side (Fig. 16). In some species (*e.g.*, *P. sordens*; cf. Berg 1950) this pattern is not very marked.

Glyptotendipes has a dark labium with a median tooth and 6 lateral teeth which gradually decrease in size laterad (Fig. 17). The paralabial plates have a crenate border, and the mandible has a dark apex with 3 distinct and dark outer teeth, and a pale inner tooth (Fig. 18). It must be recognized that other genera may have these features (*e.g.*, *Limnochironomus*) and that other species of *Glyptotendipes* may not have a labium and paralabial like those shown (cf. Lenz 1957 and Berg 1950). Hence the diagnosis of *Glyptotendipes* must be regarded as not too satisfactory.

The head capsule of *Chironomus* (Fig. 19) is readily recognized by the tripartite middle tooth and 6 lateral teeth of the labium and by the striations on the paralabial plates. These are distinct, but occur only at the base of the paralabials.

A head capsule resembling Lenz's (1957) drawing of *Parachironomus varus* was found. The labium has a median tooth and 7 lateral teeth (rather than the 6 in *Glyptotendipes*) (Fig. 20), and the mandible is rather narrow, with a dark apex and two dark outer teeth (Fig. 21). There seems to be an indistinct basal tooth. Both mandibles were present on the head found, and both had a very large and broad accessory tooth. This is not mentioned or shown by Lenz (1957).

The pattern of the teeth on the labium and their color make *Microtendipes* readily identifiable. The labium has 14 teeth; the four median teeth are shorter than the laterals, and the two most median teeth are almost colorless, whereas the other teeth are dark (Fig. 22). The striations on the paralabial plates show an alternation of heavy and faint striations. The mandible has a pale inner tooth, dark apex, and 3 dark outer teeth (Fig. 23). One head was found.

In *Paratendipes* there is also a contrast in the color of the labial teeth. In this genus, however, the median 6 teeth are short, and the median 4 teeth are pale, the others dark. There are 6 lateral teeth, for a total of 18 teeth (Fig. 24). The mandible (Fig. 25) has an apex, two outer teeth, and an inner tooth. All are rather pale. Two heads were found.

One head capsule of *Cryptochironomus digitatus* (Malloch) was found. The genus is readily recognized by the broad, toothless, pale median portion of the labium, with dark lateral teeth angled toward the median line (Fig. 26). The paralabials are rather elongate, and the mandible is narrow (Fig. 27) with an apex and 3 outer teeth. The species can be identified by the key of Curry (1958).

The tribe **Tanytarsini** can be readily recognized by the elongate striated paralabial plates, by the odd number of labial teeth, and by the

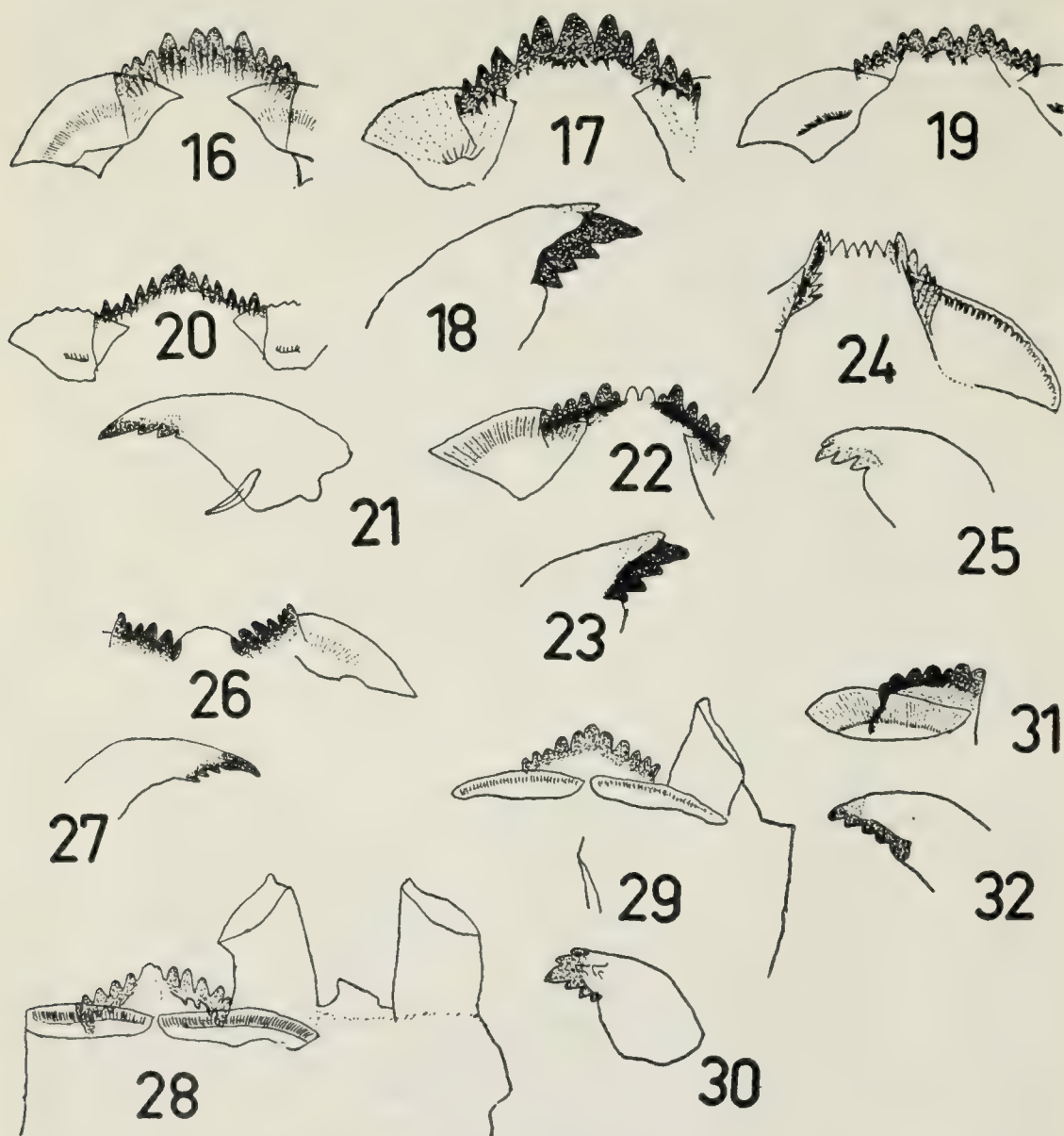


Plate II

All figures were drawn with the aid of a microprojector, at high power (440x). Scale shown in microns.

Polypedilum

16. Labium and paralabial. Core M-III. 18.35 m.

Glyptotendipes

17. Labium and paralabial. Core M-IV. 8.42 m.
18. Mandible. Core M-IV. 8.42 m.

Chironomus

19. Labium and paralabial. Core M-I dupl. 21.95 m.

Parachironomus cf. *P. varus*

20. Labium and paralabial. Core M-I. 22.20 m.
21. Mandible. Core M-I. 22.20 m.

Microtendipes

22. Labium and paralabial. Core M-IV. 11.10 m.
23. Mandible. Core M-IV. 11.10 m.

Paratendipes

- 24. Labium and paralabial. Core M-I. 27.39 m.
- 25. Mandible. Core M-I. 27.39 m.

Cryptochironomus digitatus

- 26. Labium and paralabial. Core M-I. 27.39 m.
- 27. Mandible. Core M-I. 27.39 m.

Tanytarsus genuinus group

- 28. Labium, paralabials, and antennal peduncles. Core M-I. 22.44 m.
- 29. Labium, paralabials, and antennal peduncle. Core M-I. 21.70 m.
- 30. Mandible. Core M-I. 21.70 m.

Tanytarsus connectentes group

- 31. Half of labium and one paralabial. Core M-I dupl. 21.95 m.
- 32. Mandible. Core M-I dupl. 21.95 m.

prominent antennal peduncles. The latter, however, are often not very apparent in heads recovered from the sediments. The larvae of this tribe are conveniently divided into the two groups *Tanytarsus connectentes* and *Tanytarsus genuinus*. The former has 6 lateral teeth, and the latter 5 lateral teeth. Almost all of the heads of this tribe found in the sediments were in the latter group. This group is comprised of three sections: *Paratanytarsus*, *Rheotanytarsus*, and *Eutanytarsus* (Hennig 1950, p. 232). Since only members of the last section are likely to be common in lakes, it is probable that most or all of the *Tanytarsus genuinus* head capsules from the Myers Lake sediments belong in the section *Eutanytarsus*.

This does not help much, however, as there are no less than 11 genera in the section *Eutanytarsus*! Three of these genera—*Micropsectra*, *Tanytarsus* sensu stricto, and *Lauterbornia*—have species that may comprise an important part of the profundal midge population. It is impossible to identify the genera in this section, let alone the species, without the intact antennae on the basis of the available keys. For convenience the European custom of applying the name *Tanytarsus* to all genera of *Tanytarsus genuinus* will be used frequently in this paper.

Two of the *Tanytarsus* head capsules recovered from the sediments are shown in Figures 28 and 29. The median tooth was often pale, and often had two shallow notches or "shoulders" on each side of it (Fig. 28). The number of teeth on the mandibles varied: some specimens had two dark inner teeth, and apex, and three dark outer teeth (Fig. 30).

Six half-heads of what is apparently a species of the group *Tanytarsus connectentes* were found. The 6 lateral labial teeth were much rounded, and the median tooth was rather short (Fig. 31). The paralabials were elongate, and had fine striations on them, which were stronger at the base. The mandibular teeth were very blunt (Fig. 32). It seems odd that all the remains of this form were half-heads.

All the genera of the **Tanypodinae** are identifiable from the head capsule. As pointed out earlier, a rearrangement of existing keys so that features of the head capsules alone are used as key characters is desirable for workers on subfossil remains. A key for the genera and groups of Tanypodinae is given below. The basis for this key is the paper by Lenz (1936) with modifications from Lenz (1939) and Johannsen (1937a).

Key to Tanypodinae (most useful characteristics in bold face)

1. Lingua with 6 teeth (in a few cases 5), the two middle teeth smaller than the lateral teeth; **hooked** mandibles; slender and stiletto-like superlinguae, with only slight indications of lateral teeth; a row of chitin points on each side of the lingua *Clinotanypus*
- 1'. Lingua with a different number of teeth 2
2. Lingua with 7 teeth; mandibles **curved**; otherwise similar to *Clinotanypus* *Coelotanypus*
- 2'. Lingua with 4 or 5 teeth 3
3. Lingua with 4 teeth, subequal and yellow *Psectrotanypus*, *varius* group
- 3'. Lingua with 5 teeth 4
4. Lingual teeth **subequal** and yellow; mandibles with a **thick base**; serrate superlinguae *Tanypus*
- 4'. With other characters 5
5. **No paralabial combs**; superlinguae forked, with inner fork shorter than the outer one 6
- 5'. Paralabial combs present 7
6. Lingua with middle tooth larger than first laterals *Pentaneura pilosella* of Joh.
- 6'. Lingua with middle tooth smallest. All other spp. of *Pentaneura*
7. **Serrate superlinguae** *Procladius*
- 7'. Forked superlinguae 8
8. **Hooked** mandibles; branches of superlinguae of equal length *Anatopynia*
- 8'. Curved mandibles; inner branch of superlingua shorter than outer branch. 9
9. Paralabial comb with 5 teeth *Psectrotanypus*, *trifascipennis* group
- 9'. Paralabial comb with 7 teeth *Macropelopia*

Tanypod heads from the sediments almost always have the lingua and paralabial combs present (if the latter are present in the living larva). The superlinguae and at least one mandible are usually present. The pecten is often absent. One must be careful not to mistake a pecten for a paralabial comb.

Five genera of tanypods were recovered from the Myers Lake sediments. By far the two commonest genera were *Procladius* and *Pentaneura* (cf. Table 2). A head and mandible of *Procladius* are shown in Figures 33 and 34. The lingua, superlinguae, and paralabial combs are as described in the key. The mandible is curved, and has one large inner tooth.

The lingua of *Pentaneura* is identical to that of *Procladius*, but the superlinguae are forked, and there are no paralabial combs (Fig. 35). The mandible is curved, and has two rather small inner teeth (Fig. 36).

Nine head capsules of the peculiar tanypod described by Johannsen (1937a) as *Pentaneura pilosella* were found. It is the only tanypod in which the middle tooth of the lingua is longer than the lateral teeth. As in the other members of the genus the superlinguae are forked (Fig. 37); and the mandible has two small inner teeth (Fig. 38). Four of the nine heads found were in the 8.42 m sample from sublittoral core M-IV. All the specimens found were very small, and the pecten was absent in all of them.

One head capsule of *Clinotanypus* was found. The pale lingua with 6 teeth, the more or less cylindrical superlinguae, with a few fine teeth on them, the long row of chitin points on the pecten, and the hooked mandible with one inner tooth quickly identify this genus (Figs. 39 and 40).

A couple of *Tanypus* heads were found. The pale lingua with 5 equal teeth, and the broad mandible and blunt paralabial combs identify this

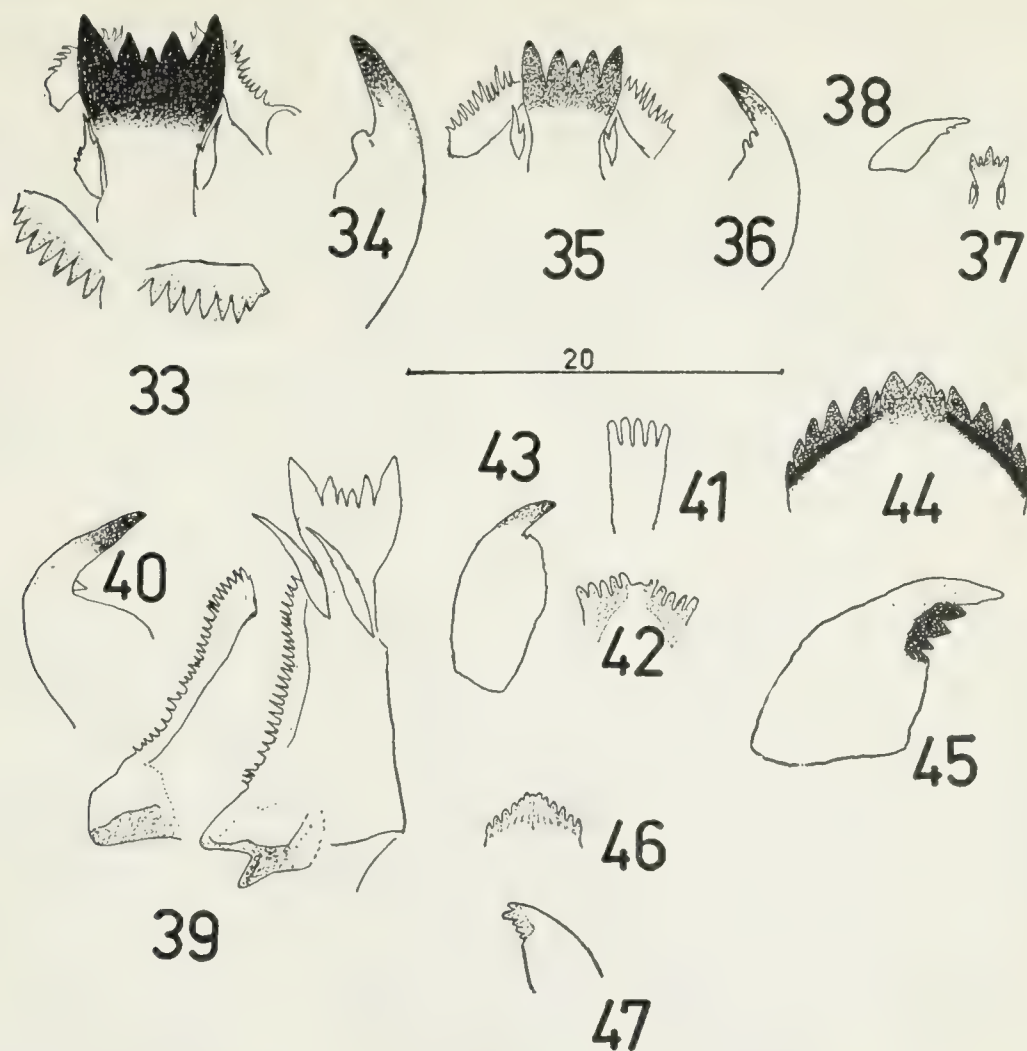


Plate III

All figures were drawn with the aid of a microprojector, at high power (440x). Scale shown in microns.

Procladius

33. Lingua, superlinguae, pecten, and paralabial combs. Core M-I. 24.70 m.
34. Mandible. Core M-I. 24.70 m.

Pentaneura

35. Lingua, superlinguae, and pecten. Core M-I. 21.95 m.
36. Mandible. Core M-I. 21.95 m.

Pentaneura pilosella of Johannsen

37. Lingua and superlinguae. Core M-IV. 8.42 m.
38. Mandible. Core M-IV. 8.42 m.

Clinotanypus

39. Lingua, superlinguae, and pecten. Core M-IV. 11.10 m.
40. Mandible. Core M-IV. 11.10 m.

Tanypus

41. Lingua. Core M-IV. 8.42 m.
42. Paralabial comb. Core M-IV. 8.42 m.
43. Mandible. Core M-IV. 8.42 m.

Orthocladiine sp. A.

44. Labium. Core M-I. 24.70 m.
45. Mandible. Core M-I. 24.70 m.

Coryoneura?

46. Labium. Core M-IV. 8.42 m.
47. Mandible. Core M-IV. 8.42 m.

genus (Figs. 41-43). No superlinguae or pecten could be seen on the specimens available.

Orthocladiinae were scarce in the Myers Lake sediments. These were recognized by the absence of paralabial plates. (Only Orthocladiinae and Tanypodinae lack these, but some Orthocladiinae have them.) Five heads of a distinctive orthocladiine were found. This is called species A. The labium has 14 teeth; the first laterals are small, and these and the median pair of teeth are slightly paler than the other teeth (Fig. 44). The mandible has a pale apex and four dark outer teeth. The basal tooth is not delimited from the mandible (Fig. 45).

Four specimens of what may be *Coryoneura* were found. These midges have a pale labium with 13 small teeth; the median tooth is noticeably smaller than the others (Fig. 46). The mandible has a prominent inner tooth, apex and outer 3 teeth (Fig. 47).

4. Identification of *Chaoborus*

All parts of the larvae of *Chaoborus* were recovered from the Myers Lake sediments, even the prelabral appendages. However, only the mandibles occur with any consistency, since they are the most heavily sclerotized part of the larva. The two species of *Chaoborus* found in Myers Lake, viz., *C. punctipennis* and *C. flavicans* (Table 1) can be distinguished on the basis of the mandible alone. *C. punctipennis* has a thin, pale tooth attached between the bases of the second and third mandibular teeth (Fig. 48). This tooth is often broken off, or not readily seen. In *C. flavicans* the attached tooth is shorter and much stouter, and is somewhat darkened (Fig. 49).

C. albatrus and *C. astictopus* have a mandible identical to that of *C. punctipennis*, and the mandible of *C. borealis* is identical to that of *C. flavicans*. These larvae are differentiated by other characteristics. Since these species are not present in Myers Lake at the present time, it seems extremely unlikely that they were present earlier and then died out.

The larva of *C. astictopus* is very similar to that of *C. punctipennis*. The only distinguishing feature, according to Cook (1956), is the length of the seta on the anterior face of the antenna. In the former species it is 0.034 mm long, and in the latter 0.021 to 0.026 mm long. This seta was measured on several of the Myers Lake larvae, and values ranging from both extremes were found. Since *C. astictopus* is restricted to the Pacific Coast, it seems that the length of the antennal seta is not a valid distinguishing characteristic.

5. Miscellaneous microfossils

Microfossils other than chironomid heads and *Chaoborus* mandibles that were quantitatively removed from the samples include statoblasts of the bryozoan *Plumatella*, ceratopogonid heads, and arachnids. The *Plumatella* statoblasts were removed only from some of the samples. This is unfortunate because the fluctuations in quantity were quite peculiar. These will be discussed under Quantitative results. Virtually no sample contained more than one ceratopogonid head or arachnid, and the distribution shows no noteworthy features. Therefore the data are

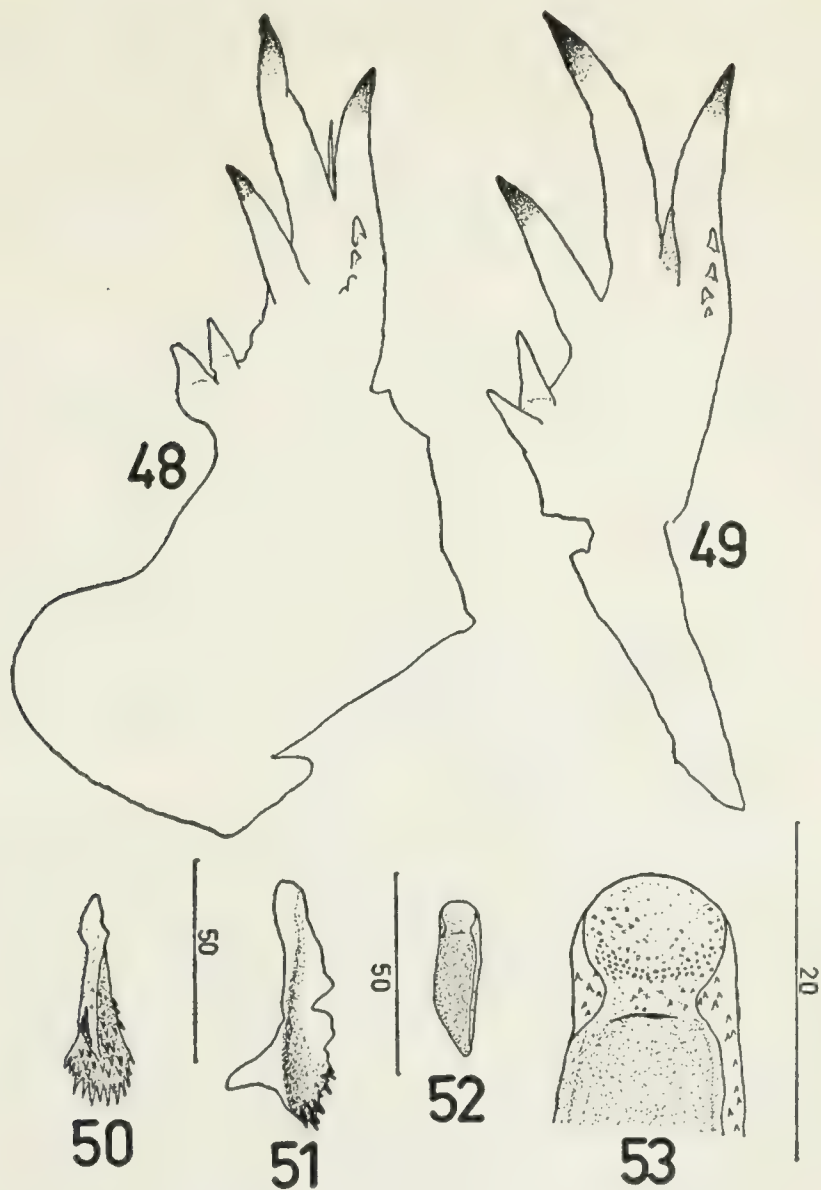


Plate IV

All figures were drawn with the aid of a microprojector, at high power (440x) unless otherwise stated. Scales shown in microns.

Chaoborus punctipennis

48. Mandible. Core M-I. 19.70 m.

Chaoborus flavicans

49. Mandible, with base broken off. Core M-I. 18.70 m.

Glyptotendipes

50. Mace of pupa. Low power. Core M-I dupl. 21.95 m.

Chironomidae

51. Anal spur of pupa. Low power. Core M-11. 23.22 m.

Tanypodinae

52. Respiratory organ of pupa? Low power. Core M-I. 21.70 m.

53. Respiratory organ of pupa? Terminal aspect at high power. Core M-I. 21.70 m.

not presented. Two kinds of ceratopogonid heads were found: one was long and slim, the other short and broad. These were not identified in any other way, however.

A couple of what are believed to be the maces of *Glyptotendipes* pupae were found (Fig. 50). Also, 3 anal spurs from chironomid pupae were found (Fig. 51), and 3 specimens of what may be the respiratory organs of tanypod pupae (Figs. 52 and 53). Three respiratory organs of *Chaoborus* pupae were found, and two of the "wheels" of Vallentyne and Swabey (1955).

6. Survey of the profundal benthos of 16 Indiana lakes

The changes that have occurred in the faunas of a lake during its developmental history are better appreciated and understood if one has a knowledge of the composition of the present faunas of that lake and of other lakes in the same region. Therefore samples of the profundal benthos were taken from Myers Lake and from 15 other lakes in northern Indiana. All these lakes are located on glacial drift of Cary subage. They are second-order, stably stratified lakes, and have moderately severe to severe hypolimnetic oxygen depletion during the summer stagnation period. Further data on these lakes may be found in previous issues of the Investigations of Indiana Lakes and Streams. The paper by Frey (1955b) is especially informative.

The samples are not quantitative; the major interest was in what kinds of chironomids and *Chaoborus* comprised the major components of the benthos. In most cases only a couple of samples were taken in approximately the deepest part of the lake with a 225 cm² Ekman-Birge dredge. Almost all of the samples contained oligochaetes, and a few tanypods were present in some of the samples. These are not considered further here, however, unless especially abundant or scarce.

Identification of the larvae to species would have been highly desirable, as closely related species may have different ecological requirements. This is emphasized especially by the work of Brundin (1949). *Chaoborus* can be identified to species in the larval stage, but the chironomids must be reared to the adult stage. Time did not permit me to rear the chironomids. In lieu of specific identification the *Chironomus* larvae have been identified to larval groups. *C. plumosus* group larvae have two pairs of long tubuli (longer than the prolegs) on the 11th segment, and a pair of short lateral appendages on the 10th segment. In the *C. plumosus* group, *semireductens* type there are two pairs of short tubuli on the 11th segment, and a pair of lateral appendages on the 10th segment. Larvae of the *C. anthracinus* group have two pairs of long tubuli on the 11th segment, but no lateral appendages on the 10th segment. A peculiar *Chironomus* larva, designated as *Chironomus* species A, had only one pair of short tubuli on the 11th segment and no lateral appendages on the 10th segment. For the sake of conciseness these larval groups will be referred to as *C. plumosus*, *C. semireductens*, *C. anthracinus*, and *C. sp. A*, respectively. It must be recognized that each of these groups may contain more than one species.

For each lake the number, date, and depth of the Ekman samples taken is given, as well as the number of larvae examined. After the

name of each lake is given the initial letter of the county in which it is located, the maximum depth in meters, and the area in hectares. The counties involved are Fulton, Kosciusko, LaGrange, Marshall, Noble, Steuben, and Whitley.

Clear Lake (S); 32 m, 310 ha. This lake was sampled on 6 Sept. 1956. A sample at 11 m had 8 *C. plumosus* larvae, and a sample at 18 m contained only 3 *Chaoborus punctipennis* larvae.

Crooked Lake (W); 33 m, 77.7 ha. On 9 Sept. 1956 two samples were taken, one at 28 m and the other at 32 m. Ten *Chironomus* sp. A larvae were found, and 6 *Sergentia coracina* larvae. The latter were not reared, but since they are identical to the head capsules recovered from the early sediments of Myers Lake, they were identified to species on the same bases as the Myers Lake head capsules. A collection by Dr. D. G. Frey at 16.5 m on 24 Oct. 1958 included 32 *Sergentia coracina* larvae and 4 *Chironomus* sp. A larvae.

Indian Village Lake (N); 6.5 m, 2.0 ha. Many samples were taken in the profundal zone of this lake. In all of them *Chaoborus* larvae were very abundant, and so were oligochaetes. Not a single chironomid was found at any time. The sediments are clayey, and leave a very small residue when sieved. Of 65 *Chaoborus* larvae examined from a sample taken 11 Sept. 1956 there were 26 *C. flavicans* and 39 *C. punctipennis* (1:1.5 ratio).

Irish Lake (K); 11 m, 54.6 ha. Two Ekman samples at 7.5 m on 10 Aug. 1956 contained 3 *Chironomus anthracinus* larvae, and numerous *Chaoborus* larvae. Of 39 of the latter that were examined all were *C. punctipennis*.

James Lake (S); 26 m, 534 ha. Just two samples were taken at 21 m on 6 Sept. 1956. These contained 8 *Chaoborus punctipennis* larvae, and just one chironomid, which was *Sergentia coracina*.

Lake Manitou (F); 14.9 m, 289 ha. The size of this lake may be somewhat misleading. There are 5 separate basins, each of which was formerly a separate lake. About 100 years ago a dam was built which raised the water level enough to form one lake from the original five. As a consequence there are large areas of shallow water in this lake, with much submersed vegetation. Specimens examined include two larvae of *Chironomus semireductens*, and 31 *Chaoborus* larvae, of which 7 were *C. albatrus*, 16 *C. flavicans*, and 8 *C. punctipennis*. The ratio of these species is thus 1:2:1, respectively.

Lake Maxinkuckee (M); 26.5 m, 751 ha. This lake was sampled 9 June 1957 at 17 m. *Chironomus semireductens* larvae were very abundant. In fact, no other organisms were observed. Evermann and Clark (1920, p. 36) stated that *Chaoborus* larvae are common in the lake.

Myers Lake (M); 18.0 m, 38.8 ha. An Ekman sample was taken at 16.5 m by W. R. Eberly on 5 Aug. 1955. He counted all the larvae therein, and found one small *C. plumosus* larva and 282 *Chaoborus* larvae (12,500/m²). Other samples were taken by me in June and September of 1957 at 9 to 12 m, and 18 m. The 9 to 12 m samples contained numerous *Chironomus plumosus* larvae (some as long as 28 mm) but few *Chaoborus* larvae; the 18 m sample contained no *Chironomus* larvae, but numerous *Chaoborus* larvae. A total of 127 *Chaoborus* larvae were examined from

Myers Lake. Thirteen of these were *C. flavicans*, and 114 were *C. punctipennis*, yielding a ratio of 1:9.

Oliver Lake (L) ; 28.5 m, 145 ha. On 7 Sept. 1956 two Ekman samples were taken, one at 16 m and one at 27 m. In the 16 m sample the larvae examined included 7 *Chironomus anthracinus*, 15 *Sergentia coracina*, 9 *Tanytarsus genuinus*, and 7 *Chaoborus punctipennis*. Oligochaetes were numerous. In the 27 m sample 25 *Chironomus* sp. A larvae were found, and numerous *Chaoborus* larvae. Twenty-one examined were all *C. punctipennis*. Again, oligochaetes were numerous. On 24 Oct. 1958 a collection was made by D. G. Frey at 20 m. Of the larvae sent to me 11 were *Chironomus* sp. A, 1 was *Sergentia coracina*, and 37 were *Chaoborus punctipennis*.

Shoe Lake (K) ; 9 m, 16.0 ha. Two Ekman samples were taken at 7 m. *Chaoborus* larvae were abundant; of 50 examined all were *C. punctipennis*. Not a single chironomid or oligochaete was seen. The sediments of this lake contained much coarse organic matter; the sieve residue was large.

Spear Lake (K) ; ca. 8 m, 16.1 ha. Two Ekman samples at 7.5 and 8 m yielded one chironomid larva, which was lost before being identified. *Chaoborus* larvae were abundant; of 85 examined 44 were *C. flavicans*, and 41 *C. punctipennis* (1:1 ratio).

Tippecanoe Lake (K) ; 37.5 m, 286 ha. This is the deepest lake in the state. The bottom fauna of this lake was investigated by Scott *et al.* (1938), who reported chironomids, *Chaoborus*, and oligochaetes in the profundal fauna. A "concentration zone" was found. The benthos in the deepest part of the lake was rather sparse. Several samples were taken at 35 m on 30 Jan. 1957. Some of the sediment was sieved and examined. The remainder was not strained, and was kept in an aquarium for several months. The sediments were almost devoid of benthos. One small oligochaete was seen, and just one *Chironomus anthracinus*, one *C. semireductens*, and 3 *Chaoborus punctipennis* larvae.

Wabee Lake (K) ; 15.5 m, 71 ha. This is a marl lake, as is Oliver Lake, but it nevertheless has marked oxygen depletion in the lower hypolimnion (Wohlschlag 1950). This author reported adults of *Chironomus plumosus* and *C. tentans*. Two Ekman samples taken at 11 and 12 m yielded 2 *C. anthracinus*, and 5 *C. plumosus*. There were also 21 *Chaoborus punctipennis* larvae.

Lake Wawasee (K) ; 23.5 m, 1200 ha. This is the largest lake in the state. The bottom fauna was studied by Scott *et al.* (1928), who reported *Chironomus tentans*, *Chaoborus*, and oligochaetes as the principal components of the profundal benthos. The weight of the organisms was over 4 times as great per unit area as in Tippecanoe Lake. Their identification of *Chironomus tentans* is very dubious, as no mention is made of rearing these larvae, and no comment on how these were distinguished from the other species of *Chironomus* that are virtually identical to it in the larval stage.

In a collection made on 12 June 1957 in 10 m of water, *Chironomus semireductens* larvae were quite abundant. Nothing else was found, not even *Chaoborus*. This is surely due to inadequate sampling.

Winona Lake (K) ; 24.4 m, 215 ha. From collections made in 17 to 19 m of water on 10 June 1957 the larvae found included 6 *Chironomus plumosus* (the tubuli were somewhat shorter than usual in this group), 3 *C. anthracinus*, and 8 *Chaoborus* larvae, of which 4 were *C. flavicans* and 4 *C. punctipennis* (1:1 ratio).

Wyland Lake (K) ; ca. 6 m, ca. 3 ha. Two samples were taken at 5.5 m on 12 Aug. 1956. One *Chironomus plumosus* larva was found, 6 *Chaoborus albatrus*, and 3 *C. flavicans* (2:1 ratio). Oligochaetes were numerous. The bottom fauna of this lake has been studied intensively by S. D. Gerking for two summers, but the results of this are not yet published, and samples of the profundal fauna were not available for examination.

The distribution of these larval groups and species in the lakes investigated is summarized in Table 1.

TABLE 1. Principal components of the profundal benthos
(exclusive of oligochaetes) in 16 Indiana lakes

Lake (Co.)*	<u>Chironomus groups</u>					<u>Chaoborus spp.</u>		
	<u>Sergentia</u> <u>coracina</u>	<u>sp. A</u>	<u>anthracinus</u>	<u>plumosus</u>	<u>semireductens</u>	<u>albatrus</u>	<u>flavicans</u>	<u>punctipennis</u>
Clear (S)				x				x
Crooked (W)	x	x						
Indian Village (N)							x	x
Irish (K)			x					x
James (S)	x							x
Manitou (F)					x	x	x	x
Maxinkuckee (M)					x			**
Myers (M)				x			x	x
Oliver (L)	x	x						x
Shoe (K)								x
Spear (K)							x	x
Tippecanoe (K)			x		x			x
Wabec (K)			x	x				x
Wawassee (K)					x			**
Winona (K)			x	x			x	x
Wyland (K)				x		x	x	

* Counties are Fulton, Kosciusko, LaGrange, Marshall, Noble, Steuben, and Whitley.

** No *Chaoborus* collected, but reported by previous investigators. Species not known.

The most important result of this survey is the discovery of *Sergentia coracina* larvae living in three Indiana lakes. Especially significant is the fact that the three lakes which have this species are the very three lakes of those studied which have the most oxygen in the hypolimnion (Frey 1955b). This helps confirm the identification of the larvae as *Sergentia coracina*, as one would expect this species to be able to survive

under moderately severe oxygen depletion, but not under severe oxygen depletion.

Moreover, if these are *Sergentia coracina* larvae the range of this species in North America is extended southward. Most of the collections in North America are from Canada. The southernmost report in the literature is from Green Lake, Wisconsin (Townes 1945). It would seem logical for *S. coracina* to have its southern limit of distribution in Indiana, since this state is the southern limit of the cold stenotherm fishes of the family Coregonidae (Frey 1955b). The final confirmation of the identity of these larvae awaits the identification of reared adults. As yet no such adults have been obtained.

The fact that the two lakes from which *Chironomus* sp. A were collected are lakes which also have *Sergentia* indicates that this species has ecological requirements similar to those of *Sergentia*. It seems to favor a greater depth, however.

Tanytarsus larvae were collected only from Oliver Lake, at the 16 m level. Since all *Tanytarsus* species are polyoxybionts, their presence supports the belief that oxygen was higher in this lake than in the others investigated, and that *Sergentia coracina* and *Chironomus* sp. A tend to have higher oxygen requirements than *Chironomus plumosus* and related species.

Chironomids in all other lakes having them were of the genus *Chironomus*. Probably at least three species of this genus are present. Although not all species of *Chironomus* have a tolerance to strong oxygen depletion it is this genus which contains the species that do have the strongest resistance to low levels of oxygen. The absence of chironomids in two lakes, Indian Village and Spear Lakes, may be due to oxygen levels too low for anything but *Chaoborus*. It is interesting to note that these two lakes offer a contrast in their sediments: in Indian Village Lake the amount of coarse organic matter is very low, whereas in Spear Lake it is very high.

Chaoborus punctipennis is present in almost every one of the lakes sampled. Its absence from Crooked and Wyland lakes is probably the result of inadequate sampling. The association of *C. flavicans* with *C. punctipennis* in 5 of the lakes poses a problem in interspecies competition. In such a mixed-species population one of the species may become extinct eventually, especially if the two species are ecological equivalents. Or, the two species may be in equilibrium, particularly if their niche is somewhat different (Allee *et al.* 1949, p. 369). The variation in the ratio of these two species to each other among the different lakes suggests that *C. flavicans* may be replacing *C. punctipennis*. Thus in Myers Lake the ratio of *C. flavicans* to *C. punctipennis* is 1:9; in Indian Village Lake it is 1:1.5; in Spear and Winona Lakes it is 1:1; and in Lake Manitou *C. flavicans* becomes dominant, with a 1:0.5 ratio.

In Lake Manitou a third species, *C. albatu*s, is present. It is only half as abundant as *C. flavicans*. Could it be that *C. flavicans* gradually replaces *C. punctipennis* as the lake matures, and that as *C. flavicans* becomes dominant it begins to be replaced by *C. albatu*s? The data from Wyland Lake tend to support this view, since *C. albatu*s is twice as abundant as *C. flavicans*, and *C. punctipennis* seems to be absent. The

numbers of larvae collected are too few to consider this as anything more than speculation, however.

7. Qualitative changes

Qualitative changes will be dealt with in the following way: the distribution of *Sergentia* in core M-I and in the other cores will be considered; then the differences in the other chironomids; and finally the changes that have taken place in *Chaoborus* distribution in these cores.

In core M-I *Sergentia coracina* heads were found in all samples from 21.84 m to 27.39 m (Table 2 and Fig. 54). They were dominant (35-86% of all chironomid heads) in all samples from 27.39 m to 22.20 m. None of the samples above 21.84 m contained a single *Sergentia* head, even though three samples were taken just 14 cm above this level, at 21.70 m. Three points about these results should be noted: (1) *Sergentia* was dominant even in the lowermost samples; other members of the *Tanytarsus lugens* community (or their Nearctic counterparts) either were not present or were scarce; (2) *Sergentia* retained its position as the dominant profundal midge for a considerable portion of the lake's ontogeny; and (3)

TABLE 2. Number of principal microfossils per ml of wet sediment and percentage of chironomids that are *Sergentia*. *Chaoborus* reported as occurrences (mandibles/2)

Core	Depth (m)	<i>Sergentia</i>		Polypedilum	Glyptotendipes	Chironomus	Tanytarsus	Pentaneura	Procladius	All Tanytarsus	Other Chironomids	All Chironomids	<i>Chaoborus</i>			Plumatella statoblasts
		No.	%										punctipennis	flavicans	All	
M-III	18.35*			2		1	2	2		4	3	12	6	0.5	6.5	
M-I	18.70						1	1	3	5	2	8	11.8**	4.7**	16.5**	13
	19.70				1	1	3		1	2	1	8	14.5	3.5	18.0	9
	21.70#			0.3	0.7	0.3	2.0	2.0	1.3	4.0	2.7	10.0	1.7		1.7	
	21.84	1	8	2		1	5	1	1	3	1	13	5		5	
	21.95	2	22			1	2	1	1	3	1	9	6.5		6.5	
	22.20	6	35	3		1	1	1	1	2	4	17	4		4	
	22.34	9	64	1	1				1	1	2	14	7		7	
	22.44	6	60	1			1		1	1	1	10				
	22.74#	11.0	73	0.5			0.5	0.5	1.0	1.5	1.5	15.0	1.2		1.2	31
	23.70	4	67						1	1	1	6				0
	24.70	3	37					1	1	2	3	8				8
	25.70	12	86					1	1	2		14	0.5		0.5	48
	26.70	17	68			2	1		2	2	3	25				63
	27.39	3	37				1		2	2	2	8				
M-I dupl	21.95#	2.5	42			1.0	1.0				1.5	6.0	4	0.2	4.2	
M-II	22.18	1	8		1	1	5	1		3	2	13	13			13
	23.22	2	25	1			1	1	2	3	1	8				
	24.87	5	33	2	1	2	4		1	2		18				
M-IV	8.42			8	5	4	15	7	15	28	15	65	1			1
	11.10			21	3	1	17	7	4	13	8	63				
Tippe- canoe	42.80	38	59			1	7	6	2	9	9	64				

* This sample is considered equivalent to 17.35 m in core M-I.

** Multiplied by 1.57 because wider mesh sieve used.

Numbers in these samples are means of replicate samples (cf. Table 3).

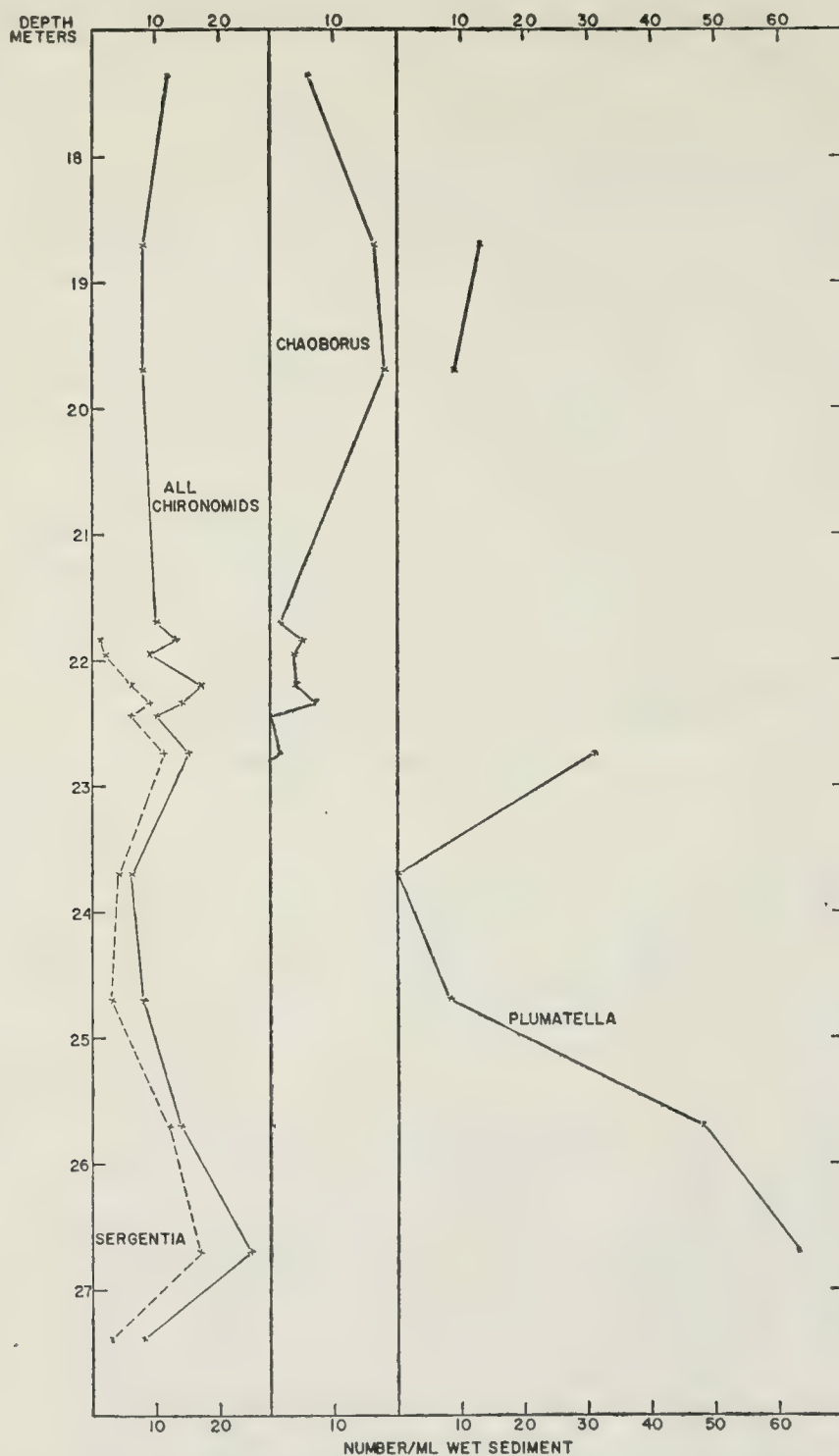


FIG. 54. Number of principal microfossils (all chironomid heads, *Sergentia* heads, *Chaoborus* spp. occurrences, and *Plumatella* statoblasts) per ml wet sediment in core M-I.

once *Sergentia* disappeared it did not come back, *i.e.*, it was present consistently below 21.84 m, and absent consistently above this level.

Comparison of the data from profundal core M-II with those from core M-I is made difficult by the differences in the depth of the water at the sampling sites, and by the uncertainty concerning the accuracy

with which the depth of water was measured. All three samples from core M-II contained *Sergentia* (Table 2). This is not surprising for the two lower samples (at 23.22 and 24.87 m), but it is surprising for the 22.18 m sample. This is because the water was supposedly 1.27 m deeper at the site of core M-II than at M-I (18.57 m to 17.30 m). Thus the 22.18 sample would be at a level equivalent to 20.91 m in core M-I! Does this mean *Sergentia* was present in very much reduced numbers above the 21.84 m level in core M-I, and that this one head found in core M-II had a very low probability of being found? The only way of checking this explanation would be to take more samples from core M-II, and find out more precisely where *Sergentia* did disappear in this core.

Core M-III was taken in 18.30 m of water. Just one sample was taken 5 cm below the surface of the sediment. This should be equivalent to the 17.35 m level in core M-I. It is considered as such, and as expected *Sergentia* is absent.

No *Sergentia* heads were found in the two samples from sublittoral core M-IV. The earlier sediments might not be present in this core, even though the original basin of the lake was reached. The steepness of the bottom slope at this site is so great that earlier sediments may have been eroded away. Only pollen analysis could settle this matter.

Although only one sample was taken from the Tippecanoe Lake core, the results from it are most illuminating. *Sergentia* comprised almost 60% of the head capsules recovered (Table 2). This suggests that Tippecanoe Lake may have had a history similar to that of Myers Lake.

Head capsules of *Chironomus*, *Tanytarsus genuinus* group, *Polypedilum*, *Glyptotendipes*, and Tanypodinae occur in small numbers (0-5 per sample) in core M-I. These heads seem to occur with greater consistency in the upper sediments beginning about 22.20 m—about the time *Sergentia* disappears. In view of the low numbers of heads it seems significant that they occur with such consistency. All of these forms have littoral species. Only *Chironomus* and *Tanytarsus* contain species that can occur abundantly in the profundal zone. All species of the latter group that live in the profundal zone are polyoxybionts. The scarcity of *Tanytarsus* remains in the lower sediments strongly suggests that the oxygen content of the hypolimnion was too low even when these sediments were laid down for any of these polyoxybiont species to survive. Those *Tanytarsus* heads found must represent littoral species whose remains were redeposited from shallower water.

It is somewhat surprising that *Chironomus* heads are not more abundant in the upper sediments of core M-I, since larvae of this genus are abundant in the upper profundal of Myers Lake at the present time. This might be because (1) the larvae are scarce in the lower profundal, or (2) the larvae of the other forms, especially *Tanytarsus*, are so much more abundant in the littoral zone than *Chironomus* is in the upper profundal that the absolute number of *Tanytarsus* reaching the lower profundal sediments is greater than the absolute number of *Chironomus*.

The data from sublittoral core M-IV support the hypothesis that redeposition accounts for the presence of *Tanytarsus*, *Polypedilum*, and *Glyptotendipes* heads, and at least some of the *Chironomus* and tanypod heads, for all of these forms are more abundant in core M-IV and com-

prise a larger percentage of the chironomid remains. The composition of the two samples from core M-IV is similar except for *Polypedilum* and *Procladius*. Just why *Polypedilum* should be so much more abundant in the 11.10 m sample and *Procladius* so much more abundant in the 8.42 m sample is not known. *Tanytarsus*, *Glyptotendipes*, and *Pentaneura* have quite similar numbers.

In core M-II and in the Tippecanoe Lake core these other chironomids form a relatively minor component of the fauna, just as in core M-I.

The distribution of *Chaoborus punctipennis* in core M-I is roughly the reciprocal of *Sergentia*'s (Table 2 and Fig. 54). It may have been present in small numbers during the early history of the lake, as the one mandible found at 25.70 m indicates. The species did not become well established until the 22.34 m level, however. Note that *Sergentia* was still the dominant chironomid at that level.

Apparently *C. flavicans* did not enter the lake until appreciably later than *C. punctipennis*, as no mandibles were found until the 19.70 m level. These results cannot be regarded as conclusive, however, as *C. flavicans* is only one-tenth as abundant as *C. punctipennis* at present (cf. p. 70), and hence the probability of finding mandibles of the former species in the sediments is much smaller. If enough samples were taken it should be possible to find out for certain when *C. flavicans* entered the lake. Also, it should be possible to see if there has been a change with time in the ratio of these two species to each other.

8. Other studies

Of the other investigations that have dealt with the chironomid remains in lake sediments those by Deevey (1942) and Frey (1955a) are particularly significant, because they are the only studies that have been made on stably stratified lakes. Both Deevey and Frey found a fauna consisting predominantly of *Tanytarsus* in the early stages of the lakes they studied.

Deevey's evidence for *Tanytarsus* dominance is less than conclusive. In core L-9 from Linsley Pond, which was taken "below the thermocline," the sample at the 28 ft level had 7 times as many *Tanytarsus* heads as any of the other samples. A total of 68 chironomid heads were found in this sample, of which 49 (72%) were *Tanytarsus*. Two feet farther up in core L-9 Deevey found only four *Tanytarsus* heads, which comprised only 18% of all chironomid head capsules. Two feet below the sample at 28 ft only three chironomid heads were found, and two of these were *Tanytarsus*. The percentage of *Tanytarsus* heads ranged from 12 to 50 in the other samples in core L-9.

Results from Deevey's L-10 core are confusing. The primary reason for this confusion is the fact that the four lowermost samples were not exactly 1 ml of wet sediment. Deevey does not say how much these samples deviate from 1 ml, yet these data were plotted on his graphs. It is impossible to calculate the percentage of *Tanytarsus* remains.

It is obvious that core L-10 shows no striking *Tanytarsus* maximum as did L-9. However, in light of Deevey's rather wide sampling interval, (generally 2 ft or 61 cm) it is possible that the *Tanytarsus* maximum was simply missed in that core.

This explanation becomes more plausible when Frey's (1955a) results from Långsee are examined. Only 0.1 ml of wet sediment was used for each sample. Nevertheless, each sample (with one exception) contained several heads. Samples were taken at 10-cm intervals. The seven samples thus spanned a distance of 60 cm. The lowermost sample, taken in clay sediment, had no chironomid remains. The uppermost sample was taken in gyttja. All the samples in between were taken in calcareous silt. This silt zone was apparently marked off rather distinctly from the other sediments, and had such a large number of remains that they were noticed as dark spots in a grayish matrix when the core was extruded. This calcareous silt was laid down in late-glacial time, judging from the pollen diagram.

In each of the five samples that were taken in the calcareous silt *Tanytarsus* comprised over 80% of the total number of head capsules. In the uppermost sample, from the gyttja zone, *Tanytarsus* comprised only 28.6% of the total chironomid head capsules. It seems that the *Tanytarsus* maximum, although well developed, was relatively short-lived. It would be interesting to re-examine a deep-water core from Linsley Pond to see if a similar sharp maximum occurs.

In summary, of three stably stratified lakes whose sediments have been examined for chironomid remains, two have shown a brief phase in which *Tanytarsus* was dominant, and the third, Myers Lake, has shown a dominance of *Sergentia* from the earliest stage until well along in the development of the lake. *Tanytarsus* was never dominant in Myers Lake. In fact, all of the other members of the *Tanytarsus lugens* community (Brundin 1956; see Discussion) were absent.

Possibly had the sediments of Myers Lake been penetrated to the glacial drift a *Tanytarsus lugens* community would have been found, but this is unlikely, as the pollen diagram indicates that the sediments obtained extend back into late-glacial time (i.e., before the Two Creeks or Alleröd Interval).

Andersen (1938), Deevey (1955a), and Livingstone *et al.* (1958) all studied the sediments of relatively shallow (ca. 2 m deep) lakes. Significantly, every one of these shallow bodies of water contained the remains of *Dryadotanytarsus*. The four places from which *Dryadotanytarsus* has been reported are (1) a Danish bog (Andersen 1938); (2) the Upper Swamp Deposit of the Pyramid Valley, New Zealand (Deevey 1955a); (3) Eight Lake, in the Brooks Range of northern Alaska (Livingstone *et al.* 1958); and (4) Whitrig Bog, Scotland (Livingstone *et al.* 1958). The genus at present is known only from the larval remains.

Eight Lake, the only one of these lakes which is located in an environment that is arctic at the present time, apparently has *Dryadotanytarsus* living in it now, as the remains were found in the uppermost sediments of the lake.

Two species have been described: *D. edentulus* by Andersen (1943), and *D. duffi* by Deevey (1955a). The *Dryadotanytarsus* remains from Eight Lake and Whitrig Bog were not identified to species.

Aside from the finds of *Dryadotanytarsus* in the sediments of unstratified lakes the work of Andersen's is the only one that considered the identification of the other chironomid remains to more than family.

Since Andersen was thoroughly familiar with the taxonomy of the Chironomidae, his identifications are relatively precise. He took samples from four levels: one in the Lower Dryas period, one in the Alleröd, and two in the Upper Dryas period. The postglacial sediments were not sampled.

There were 9 species or groups that occurred in enough abundance to permit them to be dealt with on a percentage-of-occurrence basis. Heads of *Dasyhelea* sp. (a ceratopogonid) and of the *Tanytarsus inermipes* group were found only in the Alleröd samples. Andersen found 7 heads of *Dasyhelea*, and 11 heads of *Tanytarsus inermipes*, which comprised 18 and 28% respectively, of the total number of heads found in that sample.

Dryadotanytarsus, *Microtendipes*, and *Chironomus* were found only in the Dryas horizons. The numbers of heads picked out at each level were rather small. Nevertheless, particularly in the case of *Chironomus* and *Dryadotanytarsus*, the numbers are adequate for believing that there was a definite influence of climate on the composition of the chironomid fauna of this small lake.

Since many species of *Chironomus* are indistinguishable in the larval stage, not much can be drawn from the distribution of the *Chironomus* heads. The *Dryadotanytarsus* remains are, of course, distinctive, and show clearly that climate must have affected the distribution of this species. Frey (1958) found a similar influence of climate on the composition of Cladocera in Wallensen, Germany, which is a shallow extinct lake much like Andersen's bog.

Peculiarly, *Cricotopus* was found only in the lower sample from the Younger Dryas. At this level the 23 heads found comprised 40% of all chironomids found! Andersen offered no explanation of this distribution, and I cannot think of one either.

Quantitative results

The best method of expressing quantities of microfossils is as number per unit surface per unit time. Livingstone (1957) and Livingstone *et al.* (1958) were able to do this for a few lakes on which they had pollen analyses and radiocarbon dates. A preliminary attempt has been made to express the quantity of chironomid heads/cm²/year in core M-I.

Usually the quantity of microfossils is expressed as number per ml of wet sediment. Variations in the rate of sedimentation and in the water content of the sediments will affect the number of microfossils found in one unit volume of wet sediment. These variations are particularly difficult to evaluate in carbonate-rich sediments. These shortcomings are unfortunate, but with the data at hand it seems best to express the microfossils as number per ml of wet sediment.

1. Effects of sieving

Since all the samples were strained, it is necessary to consider any effects this procedure may have had on the number of remains recovered. These effects can best be evaluated from the data on the 19.70 m sample (Table 3). Whereas all the other samples (except at 18.70 m) were strained just once through the 0.125 mm sieve, the 19.70 m sample

TABLE 3. Number of Chaoborus mandibles retained by sieves with apertures of 0.240, 0.203, and 0.125 mm

<u>Aperture</u> (mm)	<u>Chaoborus spp.</u>			<u>Chaoborus punctipennis instars</u>					
	S	P	Occur- rences	<u>2nd</u>		<u>3rd</u>		<u>4th</u>	
				S	P	S	P	S	P
0.240	8	2	6			4		2	1
0.203	7	2	5.5	1			2	5	
Sub total	15	4	11.5	1		4	2	7	1
0.125	11	1	6.5		1	4	1	4	
Total	26	5	18.0	1	1	8	3	11	1

S = singles; P = pairs; Occurrences = mandibles/2.

was strained through three sieves of different mesh apertures, *viz.*, 0.240 mm, 0.203 mm, and 0.125 mm.

It is obvious that a considerable number of mandibles passed through the 0.240 mm and 0.203 mm sieves. Note, however, that each size of sieve retained about the same number of mandibles. If the number of mandibles retained were a strict function of mandible size one would expect a marked difference in the number of mandibles retained by each sieve. This lack of a marked difference thus indicates that the retention of the mandibles by the sieve is not strictly a function of size. It is probable that any cuticle or "skin" attached to the mandible could catch on the wires of the sieve, and thus cause the retention of the mandible.

The width of the mandible varies considerably, depending on whether or not the expanded base is broken off (cf. Figs. 48 and 49). Three intact *C. punctipennis* mandibles of different sizes were measured. The smallest mandible, with a median tooth 0.090 mm long, had a maximum width of 0.19 mm; the next largest mandible, with a median tooth 0.143 mm long, had a maximum width of 0.30 mm; the largest mandible, with a median tooth 0.173 mm long, had a maximum width of 0.31 mm. Thus even the smallest mandible should be retained by the 0.125 mm sieve if the mandible is intact. If the expanded basal part is broken off, probably not even the largest mandible would be retained, as it measured only 0.093 mm across the base of the teeth.

Since the sample from 18.70 m was only strained through the 0.203 mm mesh, it was thought best to calculate a factor (from the 19.70 m sample) by which the numbers of *Chaoborus* mandibles could be made comparable to the other samples. This factor was 1.57.

2. Replicate samples

Because of the low number of chironomid heads and *Chaoborus* mandibles recovered in each sample, variations in the number of head capsules must be interpreted with considerable caution. Perhaps we can best gain an appreciation of the reliability of these quantitative results

TABLE 4. Number of chironomid heads and Chaoborus occurrences
(mandibles/2) in replicate samples

Core	Depth (m)	<u>Sergentia</u>	<u>Polypedilum</u>	<u>Glyptotendipes</u>	<u>Chironomus</u>	<u>Tanytarsus</u>	<u>Pentaneura</u>	<u>Procladius</u>	All Tanytarsus	All Chironomids	<u>Chaoborus</u>
M-I	21.70		1			1		2	2	6	3
	"					3	3		4	12	1.5
	"			1	1	2	3	2	6	12	0.5
	mean		0.3	0.3	0.3	2.0	2.0	1.3	4.0	10.0	1.7
M-I	22.74	11						1	1	13	1.5
	"	11	1			1	1	1	2	17	1.0
	mean	11.0	0.5			0.5	0.5	1.0	1.5	15.0	1.2
M-I	21.95	2			2					6	5.5
dupl	"	3				2				6	3.0
	mean	2.5			1.0	1.0				6.0	4.2

by examining the data obtained from replicate samples at the same level (Table 4).

At 21.70 m, in three samples the number of *Chaoborus punctipennis* mandibles varied from 1 to 6, a rather large amount of variation. The number of chironomid head capsules varied from 6 to 12, with two of the samples showing 12. Even this relatively small amount of variation may be exaggerated, as the sample with only 6 was counted before the method of counting had been refined to the point where centrifuge tubes and transfer pipettes were examined for head capsules that might have stuck on them.

At 22.74 m results from two samples were in surprisingly good agreement with each other. Total chironomid head capsules varied the most, from 13 to 17. *Sergentia*, however, had exactly the same number in both samples. Even the difference in the number of *Chaoborus punctipennis* mandibles is only one mandible.

The last pair of samples to be analyzed from the same level was from 21.95 m from the duplicate monolith of Myers Lake I. Again, variation is gratifyingly small in the *Chaoborus punctipennis* mandibles and in the *Sergentia* heads, and also in the total number of chironomid heads. It is surprising that no tanytarsus heads were found in either sample from this level. These are the only two samples, out of all that were taken in this investigation, that did not contain at least one tanytarsus head.

If it is assumed that the chironomid head capsules and *Chaoborus* mandibles have a Poisson distribution, then the range of 95% confidence limits can be determined from the tables of Ricker (1937). These ranges were found to overlap in every case except for the 26.70 m sample for

chironomids, and the 18.70 and 19.70 m samples for *Chaoborus*. However, it is not known whether or not a Poisson distribution accurately represents the distribution of the chironomid and *Chaoborus* remains. In view of the small variation in the replicate samples it is believed that more weight can be given to the quantitative variations than the overlap of the Poisson confidence limits would imply.

3. Instars of *Sergentia coracina* and *Chaoborus punctipennis*

In order to obtain a better idea of how validly the samples represented the actual populations of chironomids and *Chaoborus*, the number of remains of each instar of *Sergentia coracina* and *Chaoborus punctipennis* were determined.

The frequency distribution of the *Sergentia* head widths is graphed in Figure 55. The widths seem to fall into 3 groups, with the middle group (third instar) extending from 3.8 to 5.7 micrometer units.

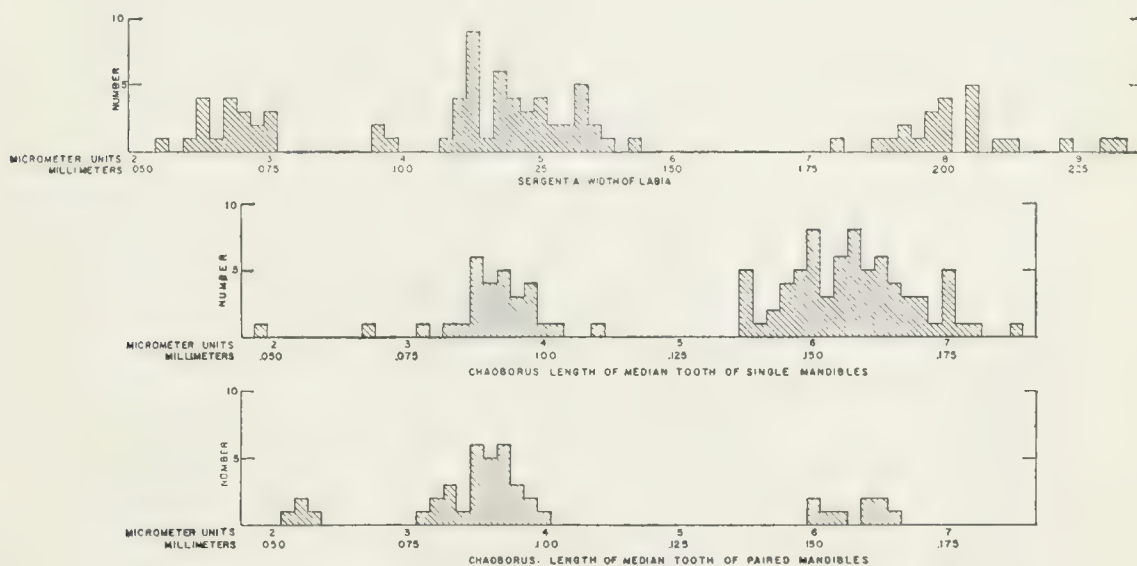


FIG. 55. Distribution of *Sergentia* labial widths and of the lengths of the median tooth of single and paired *Chaoborus punctipennis* mandibles.

To prove that each group, as delimited, really represented an instar, use was made of Dyar's Law, which states that the ratio of increase in the size is constant from one instar to the next. Factors were calculated, using the median of each group, by dividing the median of one group by that of the next smaller group. The medians are 8.0, 4.8, and 2.7 micrometer units, and the factors are 1.67 and 1.78.

These factors are quite close to each other. Moreover, the results of the application of these factors agree remarkably well with those of Rempel (1936) on *Chironomus rempeli* Thienemann [called *C. hyperboreus* Staeger by Rempel and *Tendipes anthracinus* (Zetterstedt) by Townes]. Rempel reported that the average widths of the labium of the four instars he found were 0.04, 0.06, 0.12, and 0.22 mm. These compare to 0.06, 0.12, and 0.20 mm of the three *Sergentia* instars found. If the factors are applied to the 0.06 mm labium, then the width of the labium of the first instar of *Sergentia* would be 0.038 or 0.040 mm (depending on which

factor is used). One would expect the labial widths of *Sergentia* to be similar to those of *C. rempeli* because the size of the entire larva is similar. Rempel found that final instar *C. rempeli* larvae had a body length of 10.5 to 22.0 mm. Brundin (1951) gave the average body length of final instar *Sergentia* larvae as 14.0 mm.

How can we account for the absence of the first instar *Sergentia* larvae? (1) We could assume that *Sergentia* has only three instars. This is extremely unlikely, as all chironomid larvae investigated on this point so far have had four instars (Berg 1950, Pause 1919, Sadler 1935). Moreover, according to Dyar's Law, another instar would fit in very well. (2) We could assume that the first instar *Sergentia* is not preserved, while the other instars are. This is not as unreasonable as it might seem at first. In fact, the first instar larva is so different from the other instars that Thienemann (1954, p. 234) has urged the adoption of the name "larvula" for this instar. The mouthparts of the larvula are not well developed, and the head is only weakly sclerotized. (3) We could assume that the 0.125 mm aperture of the sieve used allowed all of the head capsules of the first instar to pass through. To test this assumption it is necessary to know the width of the head capsule of the second and first instars, and we need to see if there are fewer second-instar heads than third-instar heads.

The widths of five second-instar head capsules ranged from 0.21 to 0.27 mm (Table 5). If a constant ratio between labium width and head

TABLE 5. Comparisons of labium width with head capsule width in *Sergentia*

Instar	Labium width		Head width
	Micrometer units	mm	mm
2nd	2.5	0.062	0.22
	2.6	0.065	0.22
	2.8	0.070	0.21
	2.8	0.070	0.26
3rd	4.8	0.120	0.46
	5.0	0.125	0.43
	5.7	0.142	0.51
4th	8.2	0.205	0.73
	8.4	0.210	0.68
	8.5	0.212	0.73
	8.6	0.215	0.75
	8.9	0.225	0.74
	9.3	0.232	0.85

width is assumed, then the minimum width of the first instar larval head should be $0.40/0.60 \times 0.21 \text{ mm} = 0.14 \text{ mm}$. Since the diagonal of the sieve is 0.175 mm, the aperture would be wide enough to allow head capsules of the first instar to pass through, but only diagonally.

There were 24 head capsules in the fourth instar, 44 in the third instar, and 21 in the second instar. The lower number of second instar

heads as compared to third instar heads supports the idea that some of the second instar heads were small enough to pass through the sieve (particularly if partly broken), and that probably all of the first instars could pass through. The absence of first instar *Sergentia* head capsules is best explained as a result of poorer preservation of these heads and of size small enough to pass through the 0.125 mm sieve diagonally.

How is the lesser number of fourth instar heads as compared to third instar heads to be explained? Exuviae of both instars ought to be equally well preserved. Whether the head capsules of larvae eaten by fish are or are not recognizable after having passed through a fish's gut (they probably would be recognizable), there should be no difference between the third and fourth instar unless one instar was eaten preferentially. However, any third instar larva that dies (for whatever cause) will not produce a fourth instar larva. Therefore it is believed that the difference in the number of third and fourth instar heads reflects the amount of mortality of third instar larvae.

The distribution of the instars with depth in core M-I is given in Table 6. Too much emphasis must not be placed on the discrepancies

TABLE 6. Distribution of *Sergentia* instars and *Chaoborus punctipennis* instars (mandibles) with depth in core M-I

Depth (m)	<u><i>Sergentia</i></u>			<u><i>Chaoborus</i></u>					
	2nd instar	3rd instar	4th instar	2nd instar		3rd instar		4th instar	
				S	P	S	P	S	P
18.70					1	1	4	10	
19.70				1		9	3	11	1
21.70							2	2	
21.70								1	1
21.70						1			
21.84		1				1	2	3	1
21.95	1	1				1	3	6	
22.20	3	4				1	2	3	
22.34	4	2	3			2	3	4	1
22.44	1	5							
22.74	3	2	6					3	
22.74		5	5			1		1	
23.70	1	3							
24.70	1	1	1						
25.70	3	8	1					1	
26.70	6	8	2						
27.39			3						

S = singles; P = pairs.

because of the small numbers of each instar. In general, the proportion of each instar is about the same at each level. It is interesting that the lowermost sample had only final instar larvae.

The most feasible measurement for obtaining the relative sizes of the *Chaoborus punctipennis* mandibles was the length of the median tooth along the anterior edge. These are graphed in Figure 55. There are quite obviously two major groups, with indications that a third group may be present in small numbers. If it is assumed that Dyar's Law would apply

to the growth of this median mandibular tooth a factor can be calculated, just as for the *Sergentia* labia.

The median length of the last instar's tooth is 6.3 micrometer units, and of the preceding instar 3.6 micrometer units. The factor obtained is 1.75. Applying this factor to the third instar value the median length of the tooth of the second instar larvae should be 2.06 micrometer units. This value agrees quite well with the small cluster of mandibles found at the lowest end of the graph. It is significant that every one of the mandibles in this group except one was paired, and that all, without exception, had part of the larval skin and other larval parts attached. These would facilitate catching on the wires of the sieve.

The measurements of the maximum width of the mandibles (cf. p. 79) further confirms the belief that most of the smaller mandibles were lost. This brings up the point that it makes a great deal of difference whether or not the expanded base of the mandibles is broken off. Although records were not kept of how many mandibles had the base broken off, it is believed that this breakage occurs rather frequently. In the majority of cases part of the mandibular fan was attached to the mandible, and other parts of the larva were rather frequently attached.

An interesting and marked discrepancy in the proportions of single and paired mandibles exists between the third and fourth instars. In the third instar the ratio of single to paired is 1:1; in the final instar, however, the ratio is 8:1. This discrepancy might be partly caused by a greater probability of final instar single mandibles being retained by the sieve. If this is the case then a large number of single third instar mandibles passed through the sieve. This seems likely. It is also possible that the larger mandibles break apart more easily than the smaller ones.

The second instar mandibles were all quite small and pale, and inconspicuous in appearance. It is conceivable that such mandibles could be overlooked in a fair number of cases, even if unstrained sediment were used.

Since the second instar larvae are so small and hard to see, it is obvious that first instar larvae would be completely absent in the 0.125 mm sieve's residue. Proof that there really are four instars of *Chaoborus* larvae is provided by Deonier (1943, p. 385), who raised *Chaoborus astictopus* from egg to adult, and described each instar. In the first instar the mandibles are well developed, but the postantennal filaments and mandibular fans are absent. Even though the mandibles are well developed, the other parts are so weakly developed that the chances of the first instar larvae being retained by the sieve or even being preserved in the sediment are negligible.

The distribution of *Chaoborus punctipennis* instars with depth (Table 6) reveals no striking differences. As with *Sergentia*, the small numbers at each level preclude more intensive evaluation.

In reporting the quantity of *Chaoborus* mandibles it has seemed most logical to divide the number of mandibles by two. The quotient is equivalent to a pair, and one pair counts as one "occurrence." Each occurrence should thus represent one larva, just as one chironomid head capsule represents one larva. By this procedure the number of *Chaoborus* mandibles is made more comparable to the number of chironomid heads.

4. Quantitative changes

Variations in the number of all chironomid heads in core M-I is largely a reflection of variations in the number of *Sergentia* heads up to the 22.20 m level (Fig. 54). The numbers of heads in the few samples above that level show no significant variation. Moreover, most of the heads in these latter samples were probably redeposited from shallower water, judging from the kinds of chironomids represented.

The number of heads per sample in core M-I ranged from 6 to 25 (Table 2). In cores M-II and M-III the numbers are within this range. Core M-IV, however, contained well over twice as many heads per sample (63 and 65). Curiously, the number of heads found in the one sample from Tippecanoe Lake was equal to the average of the M-IV samples, even though *Sergentia* was dominant in Tippecanoe Lake, and absent in core M-IV.

In core M-I it is convenient to consider variations in the quantity of *Sergentia* alone. Even though the numbers are smaller than when all chironomids are considered they may be more valid, because the "group" is more uniform. Figure 54 shows that there are two minima—at 27.39 m and from 24.70 to 23.70 m—and two maxima—from 26.70 to 25.70 m, and from 22.74 to 22.20 m.

These changes in the quantity of *Sergentia* could have four causes: (1) sampling error, (2) variations in the water content of the sediments, (3) variations in the rate of sedimentation, or (4) variations in the productivity of *Sergentia*. The differences between maxima and minima are too large to be dismissed as sampling error, despite the relatively low numbers involved, because of the results obtained from the replicate samples (Table 4). The small variation in the water content of the sediments (Table 7 and Fig. 56) is not likely to have affected the number of heads. No means of determining the constancy of the rate of sedimentation was available, although the microlaminae in several parts of the core suggest that it may have been fairly constant. There is no particular reason for believing that the rate of sedimentation varied greatly, and thus it is believed that the fluctuations in the quantity of *Sergentia* heads probably reflect changes in the productivity of that organism.

The quantitative data on *Chaoborus* must be treated more circumspectly than the data on chironomid heads, as the results from the replicate samples and instar analysis shown. Undoubtedly the figures on *Chaoborus* are too low. Apparently *Chaoborus* larvae were present in Myers Lake quite early, but did not occur in appreciable numbers until the 22.34 m level. Then the population seems to have increased considerably between 21.70 and 19.70 m, stayed high until 18.70 m, and then decreased in the latest stages of the lake's history.

In view of the predominance of *Chaoborus* in the profundal zone of Myers Lake at the present time it seems unlikely that this organism would have undergone a decrease in the most recent phase of the lake's development. The increased numbers at 18.70 and 19.70 m are believed to be due to the different treatment of the samples from these levels, and not to an increased population of *Chaoborus*.

The number of mandibles retained is believed to be partly due to the number of times the sample is strained (cf. Effects of sieving). The

sample from 19.70 m was the only sample strained more than once. A factor, derived from the results of the 19.70 m sample, was applied to the 18.70 m sample, since the latter had been strained through a larger mesh sieve than the other samples.

If the increased numbers of *Chaoborus* mandibles at 18.70 and 19.70 m are simply due to the treatment of the samples, then *Chaoborus* larvae have been as abundant as they are at present since the 22.34 m level. It is conceivable that a real decrease in *Chaoborus* did occur in the latest stages of the developmental history of Myers Lake, as Wood (1956) found that the population of *C. punctipennis* and *C. flavicans* in Little McCauley Lake, Ontario, was reduced to one-ninth of its former number the summer after heavy fertilization of the lake.

In some of the samples all *Plumatella* statoblasts were counted. The variations in the numbers of these statoblasts is noteworthy because there is a distinct positive relationship with the fluctuations of *Sergentia* heads (Table 2 and Fig. 54). In the case of the *Plumatella* results in Table 2 the blank spaces indicate levels at which no counts of *Plumatella* were made. The one level at which the sample was examined for these statoblasts but none was found (23.70 m) is indicated by a 0. No explanation can be offered for this peculiar correlation.

Cladocera were not considered in this investigation. One observation on these that is worth mentioning, however, is the presence of prodigious numbers of *Bosmina* shells in all three samples taken from the 21.70 m level. The sieve residue consisted almost entirely of these shells. In no other sample taken in this investigation was the number of shells at all comparable. Again, the significance of this large peak of *Bosmina* is not known.

It was possible to obtain a first approximation to the number of head capsules laid down per cm² per year in the upper part of core M-I. From the preliminary pollen analysis of the core it was learned that a very clearly defined pine maximum occurs at 23.35 m. This *Pinus* maximum doubtless represents the B pollen zone of Deevey (1939). Radiocarbon date of the pine zone in southwestern Michigan reported by Zumberge and Potzger (1956) ranged from 6,000 to 8,000 years B. P. Therefore 7,000 years was considered a reasonable estimate of the age of the sediments in the B zone of Myers Lake.

Since 6.05 m of sediment have been deposited since the pine maximum, the average annual rate of sedimentation has been 0.086 cm/year. The average number of chironomid head capsules above the pine maximum is 11.6, so the number of head capsules laid down per cm² per year was $0.086 \times 11.6 = 0.998$. This figure is vitiated somewhat by the fact that probably most of the heads in that part of the core above 22.20 m were redeposited from shallower water. The average number of *Chaoborus* occurrences above 23.35 m was 5.6. Therefore the number of *Chaoborus* occurrences per cm² per year was $0.086 \times 5.6 = 0.4816$. The latter figure is doubtless an underestimate, since quite likely only part of the *Chaoborus* mandibles were recovered.

0.482

5. Other studies

The principal studies that have considered the chironomid remains in the sediments quantitatively are Deevey (1942, 1955a), Frey (1955a), and Livingstone *et al.* (1958). Although Gams' (1927) study on Lunzer Obersee was not quantitative, it is still noteworthy that Gams commented on the large number of *Tanytarsus* heads in the early sediments of that lake.

In core L-10 from Linsley Pond Deevey (1942) found 0 to 21 heads per ml of wet sediment. Unfortunately none of the samples from the A-1 zone is quantitative. Core L-9 had one sample (from the A-1 zone) that contained 68 heads. The second highest number of heads found in this core was 33, up in the C-1 zone. The numbers in core L-9 average somewhat higher than in L-10, but except for the one maximum sample the difference is not great.

Why was such a large number of chironomid heads found in the A-1 zone of core L-9 and not in the A-1 zone of core L-10? There are two ways of explaining this discrepancy. The *Tanytarsus* maximum may have been so brief that Deevey's sampling interval was not narrow enough to catch it in L-10, as suggested in the previous section. Or, there may have been a larger number of chironomids living in or near that area of the lake bottom from which core L-9 was taken.

In core L-2, which was taken in only 4 m of water, the maximum number of heads per ml of wet sediment was 38. Tanypods were not particularly abundant, but *Tanytarsus* heads were in four of the samples (three of them in the A-1 pollen zone). During A-2 there was a sharp drop in the number of *Tanytarsus* heads in this core, except for the sample taken near the boundary of A-2 and C.

Since Frey (1955a) examined only 0.1 ml of wet sediment, his figures have been converted to number of heads per ml of sediment in order to make them comparable to the other data presented here. The samples in the calcareous silt zone of Längsee ranged from 60 to 370 heads per ml. The other samples, from the bottom up, had 210, 180, and 120 heads, so it is obvious that during this period the production of midges was relatively high. Evidence that these large numbers are not due to a lower rate of sedimentation is provided by the cladocera remains. Virtually no cladocera remains are found in this calcareous silt. The one sample taken in the gyttja shows a great increase in the number of *Bosmina* rostra. In this same sample the number of midge heads drops to 70, and only 29% of them are *Tanytarsus* heads. Thus there seems to be an inverse relationship between the quantity of midges and of cladocera. It is conceivable that most of the zooplankton during the silt stage consisted of copepods, which do not fossilize. This explanation would be special pleading, however.

In core M-I the number of chironomid heads per sample ranged from 6 to 25, whereas in Deevey's L-10 the numbers ranged from 0 to 21. Thus the quantity of chironomids in the two lakes seems to have been rather similar, although Myers Lake had a slightly higher quantity. This would be even more true if the differences in the technique used in measuring the samples is considered. Deevey used the displacement method, whereas

the direct measurement method was used in the Myers Lake investigation. According to the comparison of the two methods by Deevey (1955a) the displacement method yields results about 10% higher than the direct measurement method. It should be remembered too that Deevey examined his samples at 20x, whereas the Myers Lake samples were examined at 45x.

The number of all heads in core M-IV, from the sublittoral of Myers Lake, and in the profundal core from Tippecanoe Lake is over twice as great as the maximum number found in core M-I or L-10, but still considerably less than the 370 heads per ml found by Frey in Längsee.

When we turn from stratified lakes to unstratified lakes there is a striking difference in the quantity of head capsules found. In the Upper Swamp Deposit of the Pyramid Valley Deevey (1955a) found as many as 1700 head capsules per ml of wet sediment! But even this number is exceeded by the values found in Eight Lake, where Livingstone *et al.* (1958) found as many as 8,000 head capsules per ml of wet sediment! This is truly an astonishing number.

It is worthy of note that in both of these lakes *Dryadotanytarsus* was predominant. Although both lakes were (or are) unstratified, they offer two interesting contrasts. The Upper Swamp Deposit must have had a high pH, as the sediments are calcareous, whereas Eight Lake is acid (pH 4.7 on 22 August 1951), and the sediments of the Upper Swamp Deposit were laid down during a temperate climate, whereas Eight Lake is located in an area which was and is arctic.

Although the maximum numbers of heads found in the Upper Swamp Deposit and Eight Lake are very large, the minimum number per ml was zero or close to it, judging by the graphs. Moreover the numbers of head capsules found in Lake A, Alaska, by Livingstone *et al.* (1958) appear to be low.

In Eight Lake there was a sharp decrease in the number of chironomids at about the time pollen zone III began. Livingstone *et al.* (1958) noted this decline, but did not correlate it with the change in pollen. Using the data provided by the latter authors on the number of midge fragments per cm² per year in pollen zone III, and the data from Livingstone's (1955a) pollen analysis of the Eight Lake core, it is possible to calculate the average number of chironomid fragments per ml of wet sediment in pollen zone III in Eight Lake. The figure arrived at is 42, which is not much different from the numbers found in Myers Lake and Linsley Pond, and lower than the numbers found in Längsee.

Livingstone *et al.* (1958) provided the first estimates of the number of chironomid fossils laid down per cm² per year. These authors had radiocarbon dates for pollen zone III in Alaska and for pollen zones A & B, C-1, and C-2 & C-3 in Linsley Pond. The values reported are as follows:

Lake A, zone III:	1.2
Eight Lake, zone III:	6.6
Linsley Pond, C-2 & C-3:	2.3
C-1:	0.7
A & B:	0.4

The data from Linsley Pond show a nice increase in productivity of midges as the lake matures and the climate warms up. However, a closer

examination of the methods and data used by these authors for the calculations of these values leads to serious doubt of their validity. The number of heads/cm²/year have been calculated for cores L-10, L-9, and L-2. The boundaries of the pollen zones were obtained from Deevey (1939), and the length of time that each pollen zone (or group of zones) lasted from Livingstone *et al.* (1958). The results are as follows:

<i>Pollen zone</i>	<i>L-10</i>	<i>L-9</i>	<i>L-2</i>
C-3 & C-2	2.28	1.32	
C-1	0.66	1.09	
A (&B)	0.37	1.93	1.99

It is obvious that Livingstone *et al.* (1958) used Deevey's data from L-10 for their calculations. Moreover, they used the four lowermost samples, which were not quantitative. If Deevey's data from L-9 are used the picture changes appreciably. The number of heads is then less in zone C-3 plus C-2, more in zone C-1, and much greater in zone A than in the corresponding zones of L-10. Indeed, the number of heads in zone A is greater than in any other zone of L-9. If the sample with 68 heads is used, and the average annual sedimentation rate of 0.108 cm/year applied to it, then the number of heads laid down is 7.35/cm²/year.

If it be objected that L-10 is the more representative core, then Deevey's basis for maintaining that there was a dominant *Tanytarsus* population in the earliest stages of Linsley Pond's development is weakened seriously. That is, it is core L-9 which has the sample with 49 *Tanytarsus* heads (and 68 heads of all chironomids).

This sample with 68 heads, and the sample two feet above it, with 22 heads, were taken in the silt zone. Vallentyne and Swabey (1955, p. 317) suggested, on the basis of 16 layers found in the silt zone of their core, that these layers might represent annual cycles of deposition. Hence the 2.4 m of sediment in the silt zone would have been laid down in 16 years according to this interpretation. On the basis of the large number of chironomid heads found in this zone in L-9 this seems improbable. Such a rate of sedimentation would have required a midge production of 776 heads/cm²/year.

Despite the discrepancies in the number of heads laid down per cm² per year, it appears that the productivity of the midge population in Linsley Pond was about the same as, or slightly higher than, in Myers Lake. The same can be said for Lake A, Alaska. In Eight Lake, however, the chironomid fragments were at least 6 times as abundant as in the other lakes.

Since Deevey (1942) is the only investigator who has reported *Chaoborus* remains quantitatively, there is little to be said. Deevey did not strain his samples, but he picked out the *Chaoborus* remains at a magnification of only 20x. On the basis of my experience, 45x is a more suitable magnification. Even at that magnification second instar *Chaoborus* mandibles might very well be missed.

It is not clear just how Deevey counted his *Chaoborus* remains. Apparently any remain was counted as one occurrence. Thus, a pair of mandibles would count as one occurrence, as would a single mandible, or a mandibular fan, or an anal fan, or any other recognizable part of a

Chaoborus larva. All parts of *Chaoborus* larvae have been found in the Myers Lake sediments.

Chaoborus apparently first became well established in Linsley Pond toward the end of the C-1 zone (26 ft below the surface of the sediment), and increased appreciably toward the end of the C-2 zone. The uppermost sample is still 3 ft below the surface of the sediment. Deevey's results are quite consistent for this core.

The lack of *Chaoborus* remains in the upper levels of core L-9 are explicable if it is assumed that L-9 was in water too shallow for *Chaoborus*. Thus, in core M-IV (which was taken in a depth of water that is probably comparable to L-9) only two *Chaoborus* mandibles were found.

The water, carbonate, and organic matter content of core M-I

Results of the analyses of the sediments for their percentage of water, carbonate, and organic matter are presented in Table 6 and Figure 56. Two characteristics of the sediments are immediately apparent: their low percentage of organic matter and high percentage of carbonate.

Except for one sample the sediments at all levels consisted of less than 10% organic matter. The maximum is only 14.7% and the minimum a mere 0.8%. In contrast to these results are those from Linsley Pond. Deevey (1942) found that in core L-10 the organic matter comprised 40 to 50% of the dry weight of the sediment, with a maximum of 59.0%. Part of the low amount of organic matter in Myers Lake may be due to dilution with carbonate, but this is at best only a partial explanation, as the rate of sedimentation was probably about the same in Myers Lake and Linsley Pond, judging by the total depth of sediment in the lake basins.

TABLE 7. Percentages of water, carbonate, and organic matter in core M-I. Carbonate and organic matter are expressed as percent of dry weight.

<u>Depth</u> <u>(m)</u>	<u>% water</u>	<u>% carbonate</u>	<u>% organic</u> <u>matter</u>
18.35*	65.5	54.4	8.4
17.74	74.4		
18.71	71.2		
19.70	71.2		
21.70	54.9	87.2	3.9
21.84	40.4	68.1	3.4
21.95	47.2	78.0	4.5
22.20	49.6	71.3	5.1
22.44	52.9	92.5	.9
22.74	47.1	74.7	14.7
24.70**	58.0	71.2	1.8
25.70**	63.6	82.0	.8
26.03**	55.3	51.3	4.6
27.39	45.8	58.6	8.3
27.50**	46.9	50.5	6.7
27.70**	35.0	29.0	7.3

* This sample is from core M-III; it is considered equivalent to 17.35 m in core M-I.

** Whatman No. 50 filter paper used.

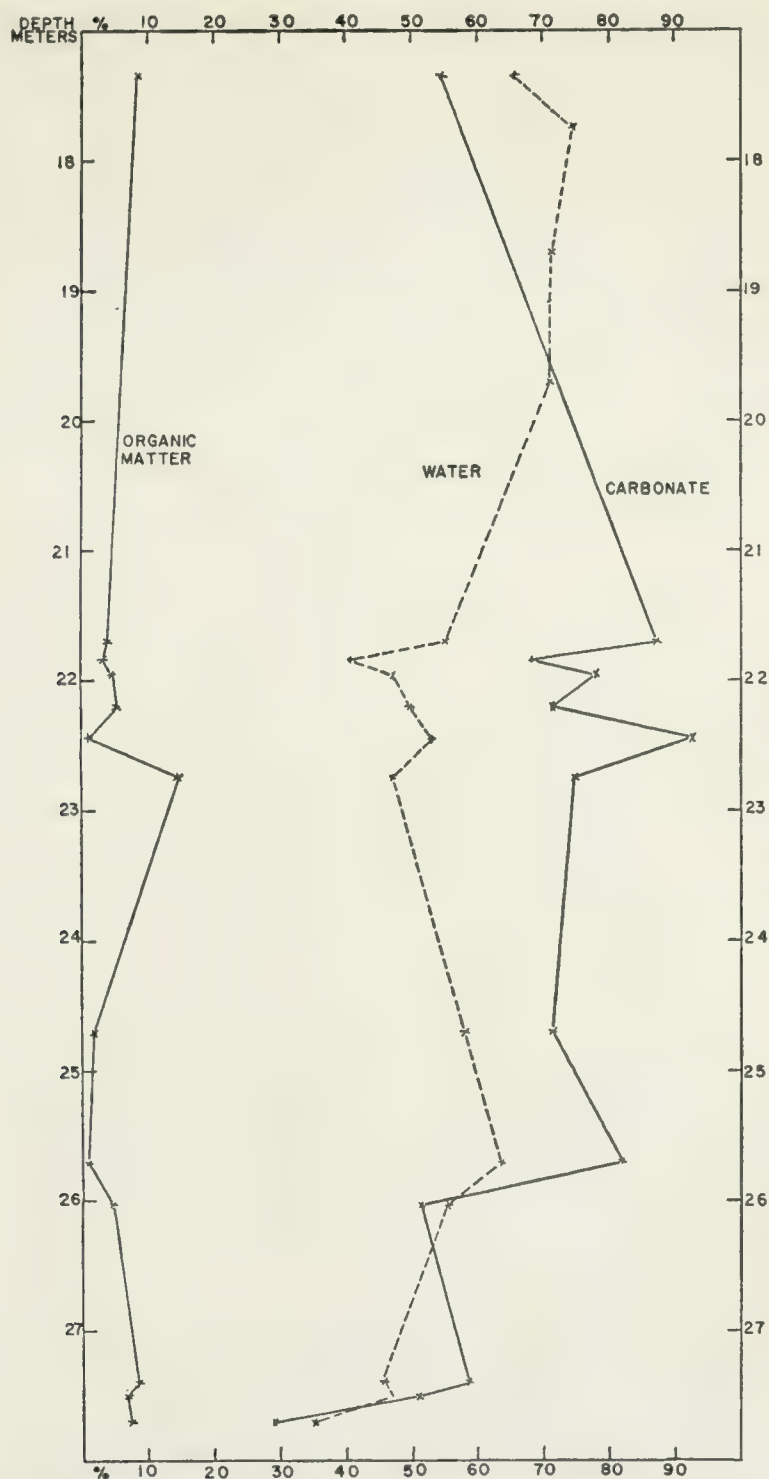


FIG. 56. Percentage of water, carbonate, and organic matter in core M-I.

There was no sigmoid increase in organic matter remaining in the sediments as the lake aged. Instead there are two minima and a maximum. One minimum lies from 25.70 m to 24.70 m, and the other at 22.44 m. The latter minimum is probably due to the high percentage of carbonate at this level. The maximum of organic matter occurs at 22.74 m, which is about where the C-1 pollen zone begins.

The percentage of carbonate varies from 29.0% to 92.5%. The minimum occurs in the lowermost sample (27.70 m). Then three stepwise

increases in carbonate occur: at 27.39 m, 25.70 m, and 22.44 m. Between 22.44 m and 22.20 m there is a rather sharp drop in carbonate, the significance of which is not known. The fluctuations in carbonate between 22.20 m and 21.70 m are interesting because four samples were taken in this area, all from the same monolith. Thus a closer sampling interval in the rest of the core might reveal more variations than the available data show. Moreover, 21.84 m is the last level at which *Sergentia* is found.

These fluctuations become even more interesting when the variations in water content are considered. Note especially that the sharp drop in carbonate at 21.84 m is paralleled by a similar drop in the water content. Since the samples above and below this level are from the same monolith, the uneven treatment of some of the monoliths would not explain the variations in this case. Why there should be a positive relationship between water content and carbonate content is not known.

The volume of the hypolimnion at different points in time

Deevey (1955b) considered the effect of reduction in the volume of the hypolimnion with age on the typology of three lakes: Linsley Pond, Grosser Plöner See, and Windermere. He concluded that mere reduction in the volume of the hypolimnion could not account for the changes in type, but that there must have been a true increase in production. This increase in production could be brought about by a more favorable climate, or by more nutrients being washed into the lake.

Change in the sediment (primarily organic matter) was the principal criterion used by Deevey for identifying conditions in the profundal zone of these lakes. Only in Linsley Pond could the chironomid fauna be used.

Myers Lake seems to have had moderately severe oxygen depletion very early in its history. No community of polyoxybiont species of chironomids ever was present, apparently. *Sergentia coracina* can withstand moderately severe oxygen depletion, yet it was eventually extirpated. It seemed desirable to see if reduction in the volume of the hypolimnion alone could account for its disappearance. Therefore an attempt was made to calculate the volume of the hypolimnion of the west basin of Myers Lake at different points in time.

According to Deevey, three conditions are necessary for computing the volume of the hypolimnion at several points in time. These are: (1) several borings at various depths of the present basin; (2) a boring at the maximum depth; and (3) a knowledge of the internal stratigraphy, so that synchronous levels can be established. The formula for calculating the volume of a slice of a sphere is used. This formula is $V = 1/6 \pi h (3a^2 - h^2)$, where V is volume, h is the height of the slice, and a is the radius of the circular surface. A correction factor is obtained by calculating the volume of the present hypolimnion with the formula and dividing the result by the true volume, calculated in the usual way.

For Myers Lake, unfortunately, all that is available is one coring at the maximum depth. Since the use of this formula is quite arbitrary at best, it may still be possible to get an idea of the changes in the volume of the hypolimnion.

Calculations were made only for the west basin of the lake, as the east basin is shallower, and the thermal stratification is not so stable (Eberly 1959). Eberly's data on morphometry have been borrowed freely. The present volume of the hypolimnion of the west basin of Myers Lake is 431,000 cubic meters. The upper surface of the hypolimnion is at 10 m, using Birge's definition of the thermocline. If we use as the radius of the surface of the hypolimnion line "a" that is on Map 1 (p. 48), then the volume of the west basin by the formula is 1,185,000 m³. Thus the spherical formula overestimates the true volume by 2.75 times.

The slope between the 5- and 25-foot contours at the place shown on the map is 0.476; from the 30-foot to the 50-foot contour the slope is much less, only 0.0794. Since the 32-foot contour is the upper limit of the hypolimnion, it seemed likely that the slope of the original basin would be closer to the slope found between the 5- and 25-foot contours at present. Accordingly, it was assumed that the slope was 0.45. Changes in the value of "a" (the radius of the surface of the hypolimnion) with increase in depth of the hypolimnion were obtained by a graph with a slope of 0.45.

The volume of the hypolimnion at the 21.80 m level and the 27.40 m level was calculated. The former level represents the depth at which *Sergentia* disappeared, and the latter level the lowermost midge sample taken (which presumably is near the original basin of the lake). The results of the calculations are:

- present hypolimnion (8 m deep): 431,000 m³;
- hypolimnion at 21.80 m (11.8 m deep): 671,000 m³ (1.56 times present volume);
- hypolimnion at 27.40 m (17.4 m deep): 1,072,000 m³ (2.49 times present volume).

These data might also be expressed in terms of percentage reduction in the volume of the hypolimnion. The results are then as follows:

- present hypolimnion is 40.2% of the original hypolimnion (59.8% reduction);
- hypolimnion at 21.80 m was 62.5% of original hypolimnion (37.5% reduction).

Wilson (1938) in his classic studies on Tippecanoe Lake and Winona Lake found a filling in of the original basin of 31.90% and 43.66% respectively. Deevey (1955b, p. 17) calculated that the reduction in the hypolimnion in each of these lakes was 36% and 49% respectively. Wilson pointed out that there is an inverse correlation between the percent of filling and the average original depth of a lake basin. Deevey's data support this last statement. According to the graph he presents on p. 17 the relatively large Grosser Plöner See and Windermere had a reduction in the hypolimnion of about 20%, while Linsley Pond, which is much shallower and smaller than the other two lakes, had a reduction in the volume of the hypolimnion of about 77%.

Since the mean depth of the west basin of Myers Lake (6.9 m) is between that of Winona Lake and Linsley Pond, the percent reduction in

the hypolimnion would be expected to lie between the values for the last two lakes. It does.

Deevey used the rate of generation of the hypolimnetic oxygen deficit to estimate when the hypolimnia of the three lakes he considered became chemically reducing. The present rate of generation of the hypolimnetic oxygen deficit in Myers Lake is not known. Such a datum would be of little use in this case, however, as Hutchinson (1957, p. 642) points out that the deficit will be in error for lakes that have an appreciable amount of photosynthesis in the metalimnion and upper hypolimnion.

It is probable that Myers Lake always has had a chemically reducing hypolimnion. This belief has three lines of support: (1) none of the polyoxybiont species of chironomids ever dominated the profundal fauna; (2) the hypolimnion may be oxygen-free as early as the middle of June at the present time; and (3) even the lowermost sediments are chemically reduced. It seems likely oxidized lake sediments would remain oxidized even after burial, as Frey (1955a) found that the holomictic sediments in Längsee were apparently oxidized *in situ*.

DISCUSSION AND CONCLUSIONS

As mentioned in the Introduction the classification of lakes by means of the species of chironomids living in the profundal zone is based on the variation in tolerance to oxygen depletion of the species concerned. Other factors may affect the community of profundal chironomids in more or less minor ways, but oxygen is the prime ecological factor. The classification is most valid for stably stratified lakes, since in these oxygen in the hypolimnion is not replenished during the summer stagnation period.

Since oxygen is the primary determinant of lake type (according to this system), it is necessary to consider what factors could cause changes in the oxygen concentration of the hypolimnion at the time of maximum summer stagnation. Basically, there are just three factors that determine oxygen concentration: the ratio of the trophogenic zone to the tropholytic zone, the amount of decomposable organic matter that is sedimented into the tropholytic zone from the trophogenic zone, and the duration of stratification.

A change in the average ratio of trophogenic zone to tropholytic zone could be produced by changes in the water level, or by filling in of the lake (at least if the trophogenic zone retains the same thickness, which is likely). There will, of course, be daily and seasonal variations in this ratio.

The duration of stratification would ordinarily be about the same from year to year in any one given lake, although unusual weather may have an important effect on duration of stratification. In particular a calm, warm spring may prevent the usual vernal circulation. This condition would be particularly important in a lake having appreciable winter oxygen depletion. In the case of Myers Lake an inhibition of vernal circulation would probably have no important effect, as the lake water contains plenty of oxygen during the winter.

The amount of organic matter produced in the trophogenic zone could

be increased, presumably, by more nutrients and more light and perhaps by higher temperatures.

The amount of nutrients available in the course of a year could be increased by two things: an increase in the proportion of nutrients taken out of the water that are returned to the water (this can be called diagenetic efficiency), and an increase in the amount of nutrients washed into the lake.

In deep lakes a greater proportion of the minerals incorporated into the plankton will be returned to the water before the dead plankton reaches the surface of the sediment. In relatively shallow lakes, such as Myers Lake, three factors will favor the return of a high proportion of the nutrients to the lake water: a chemically reduced hypolimnion, a high ratio of surface area of sediment to volume of water, and possibly a low silt content. Livingstone (1957) adduced good evidence for his belief that as the amount of inorganic matter washed into Linsley Pond decreased there was a corresponding increase in diagenetic efficiency.

Only a change in climate could produce more favorable light and temperature conditions.

To my knowledge there is no clear-cut evidence for more or "better" nutrients being washed into the lake later in its history; indeed, if Livingstone's reasoning is correct, the less matter washed in (at least if it is in the form of silt) the more nutrients are available. Deevey (1955b, p. 30) believed that "increasing geochemical maturity resulting from soil formation and the growth of forests" as well as higher temperatures were responsible for a real increase in biologic productivity in early postglacial time. "The productivity probably increased in more or less linear fashion until the end of Boreal time, when it may have been slightly higher than today owing to especially favorable light and temperature conditions."

Actually, it is usually impossible to know whether increasing diagenetic efficiency or an increase in the nutrients washed into a lake is responsible for an increase in the nutrients in the lake water.

That climate can affect the species of chironomids and cladocera living in unstratified lakes has been shown by Andersen (1938) and Frey (1958), respectively. The latter author had very rough quantitative data on the number of cladocera remains present during different climates, but these data can scarcely be regarded as proof that climate *per se* increases the quantity of cladocera. Nevertheless Thienemann (cited by Frey 1958, p. 268) pointed out that all (low altitude) tropical lakes are eutrophic and all arctic lakes are oligotrophic by accepted standards regardless of morphometry (and presumably edaphic factors). "Both Fjerdningstad's data on the algae of Bølling Sφ and the Wallensen data on the Cladocera indicate that eutrophication probably can be reversed with a reversal of the climatic and sedimentation cycles" (Frey 1958, p. 268). Deevey (1955b) also believed that climate caused a real increase in productivity. However, he placed great stress on the sigmoid increase in organic matter in Linsley Pond, which, as Livingstone (1957) showed, is probably an artifact.

Before going further, it would be well to give the latest classification of harmonic lakes of the cold and temperate areas of the northern hemi-

sphere (from Brundin 1956, p. 192; an excellent historical review of lake types based on chironomids can be found in Brundin 1949).

- I. *Heterotrissocladius subpilosus* lakes (ultraoligotrophic)
- II. *Tanytarsus lugens* lakes (moderately oligotrophic)
- II/III. *Stictochironomus rosenschöldi* lakes and *Sergentia coracina* lakes (mesotrophic)
- III. a) *Chironomus anthracinus* lakes (moderately eutrophic)
b) *Chironomus plumosus* lakes (strongly eutrophic)

In ultraoligotrophic lakes *Heterotrissocladius subpilosus* is typically the only species of chironomid present in appreciable numbers. In moderately oligotrophic lakes, however, a whole community of chironomids is present, comprised of the following species:

Protanypus morio
Monodiamesa bathyphila
Heterotrissocladius grimshawi
Heterotrissocladius määri
Paracladopelma obscura
Sergentia coracina
Stictochironomus rosenschöldi
Micropsectra insignilobus
Lauterbornia coracina
Tanytarsus lugens

These species may occur in different proportions in different lakes, but in typical oligotrophic lakes all members can be expected to be present. In order to have a convenient name for this community Brundin chose one of the species, *Tanytarsus lugens*, as the name for the community.

Since most of Brundin's work has been on ultraoligotrophic and oligotrophic lakes it is for these lakes that the specific composition of the profundal chironomid fauna is best known. It is known that *Stictochironomus rosenschöldi* and especially *Sergentia coracina* are more resistant to low concentrations of oxygen than are the other members of the *Tanytarsus lugens* community. Therefore in mesotrophic lakes both species or just *Sergentia coracina* remain, of the *Tanytarsus lugens* community.

None of the lakes in which *Stictochironomus* or *Sergentia* are dominant (Lundbeck 1936) has been as carefully investigated as the oligotrophic lakes in Sweden. Hence it is not possible to be precise about the specific composition of mesotrophic lakes; there is probably not a distinct community present, but rather just the holdovers from the *Tanytarsus lugens* community, with probably some *Chironomus* species coming in. These mesotrophic lakes are poorly characterized, both because of their transitional nature and because of the lack of intensive investigation of their profundal fauna.

The *Chironomus* lakes have not been so thoroughly investigated as the oligotrophic lakes either; hence it again is not possible to know whether there is a "community" in which *Chironomus anthracinus* or *C. plumosus* is dominant, or whether these species are the only ones.

In *Chironomus* lakes (and in some *Sergentia* lakes—cf. Lundbeck 1936) *Chaoborus* often comprises a significant part of the profundal fauna. Indeed, some lakes that have such severe oxygen depletion that even *Chironomus plumosus* is extirpated may still have considerable populations of *Chaoborus*.

Four drawbacks to this schema of lake classification must be borne in mind.

One drawback is that chironomids may form only a minor component of the profundal fauna in some cases. *Chaoborus*, in particular, may quite commonly exceed chironomids in number and in weight, although oligochaetes may be dominant or even the amphipod, *Pontoporeia affinis*, in some very deep and oligotrophic lakes.

Secondly, once the oxygen content becomes low enough to exterminate the chironomids any further increase in production (and hence in the amount of organic matter decomposed in the hypolimnion) will not be detectable on the basis of profundal midges. Conceivably the species of *Chaoborus* could be used here.

Thirdly, environmental factors other than the quantity of oxygen are not taken into account. Temperature will, of course, be relatively constant and cold if the lake is stably stratified. The amount of "humus" in the water and the sediment is significant only for dystrophic lakes, which need not be considered here, as Myers Lake is a harmonic lake. Conceivably the concentration of carbon dioxide could be significant, although this would, in general, be the reciprocal of the oxygen concentration. What may be particularly significant is the composition of the substrate in which the organisms live. Virtually no work has been done that has considered the relationship of the chironomids to the finer constituents of the sediments. The physical structure of the bottom might also play a role.

Finally, this schema is based on Palaearctic species. In 1945 Townes found that 33 species of Chironomini were Holarctic in distribution. However, Townes says (p. 3): "It is probable that a considerably larger number are of Holarctic distribution, and more comparisons should be made between the species of the two faunas. In the preparation of this paper the possibilities for comparison were restricted by a dearth of Palaearctic material." Towns reported *Sergentia coracina*, *Chironomus anthracinus*, and *Chironomus plumosus* in the Nearctic region. He described several new species of *Stictochironomus*. Possibly one of these would be *Stictochironomus rosenschöldi*, if material were available for comparison. Thieneman (1954, p. 505) summarizes the species of lake-dwelling chironomids known to live in both the Nearctic and Palaearctic regions. *Monodiamesa bathyphila* is the only other species in the *Tanytarsus lugens* community that has been reported from the Nearctic. This is surely not significant for the species that are not Chironomini, however, as no comprehensive treatment of the other groups is available for the Nearctic region. It is worth mentioning here that Brundin (personal communication) found larvae in the profundal of Lake Cayuga, New York, that he believed were *Heterotrissocladius subpilosus*. A comprehensive study of the chironomid fauna of a North American oligotrophic lake has yet to be published.

For Myers Lake the three questions that need to be answered are: (1) why *Sergentia coracina* was dominant from the beginning of the lake's history; (2) why *Sergentia* disappeared; and (3) why no species of *Chironomus* ever dominated the lower profundal fauna after *Sergentia* was eliminated. The first question presupposes that core M-I nearly reached the original basin of the lake. This seems likely.

On the basis of Brundin's classification the answer to the first question could only be that even in the earliest stages of the lake's history the oxygen concentration of the hypolimnion became so low during summer stagnation that the other members of the *Tanytarsus lugens* community were unable to survive.

The fact that even the lowermost sediments of the lake were reduced may offer some support to the above-stated belief, as Frey (1955a) reported that the holomictic sediments of Långsee exist in an oxidized condition whereas the meromictic sediments are reduced.

The answers to questions (2) and (3) are both connected with an increase in the annual hypolimnetic oxygen deficit. There must have been an increase in the deficit, but one wonders whether it was a relatively rapid increase, or a gradual increase.

What evidence indicates that a gradual and steady increase in the annual hypolimnetic oxygen deficit took place?

Sergentia coracina larvae have been found living in the profundal of three Indiana lakes: James, Oliver, and Crooked Lakes (Table 1). Significantly, these are the very three lakes out of all those so far sampled in Indiana that have the most oxygen remaining in the hypolimnion during summer stagnation (Frey 1955b). Moreover, *Sergentia* was dominant at one time, and has since died out, in at least one other Indiana lake, viz., Tippecanoe Lake (Table 2).

Finally, the belief that a warmer climate is mainly responsible for an increase in productivity of a lake is not borne out by the data from Myers Lake. That is, there is no correlation of the disappearance of *Sergentia* with the amelioration of climate. Oak was well established in the watershed when the sediments at 22.88 m were laid down, but *Sergentia* continued dominant until the 22.20 m level, and did not disappear until the 21.84 m level. Furthermore, core M-I extends back into late-glacial time, and yet *Sergentia* was dominant then and throughout the Two Creeks Interval.

What evidence indicates that a rapid increase in annual hypolimnetic oxygen deficit took place?

The only evidence from the present study was the failure of *Chironomus* to become dominant in the lower profundal after *Sergentia* had died out. In other words the stage of moderate eutrophy seems to have been skipped (using eutrophy in the sense of hypolimnetic oxygen depletion). *Chironomus* is abundant in the upper profundal of Myers Lake at present, however, and probably became so at about the time that *Sergentia* died out, as evidenced by the consistent occurrence of low numbers of *Chironomus* heads from 22.20 m on up. Myers Lake could be correctly called a *Chironomus* lake at the present time, since *Chironomus* need not be dominant in the lower profundal for the lake to be a *Chironomus* lake.

Other studies, particularly that of Deevey (1955b), have indicated that there is a real increase in productivity in postglacial time, and hence an increase in the annual hypolimnetic oxygen deficit. This increase would be greater than that due to reduction in the volume of the hypolimnion. Most significant is the apparently true sigmoid increase of *Bosmina* in Linsley Pond. This increase of *Bosmina* is correlated directly with the decrease in inorganic sedimentation. If there was a real increase in the production of *Bosmina* then there should have been a real increase in the amount of decomposable organic matter being sedimented into the hypolimnion, and hence an increase of the hypolimnetic oxygen deficit. Perhaps Linsley Pond is a special case. At least Myers Lake differs in that there was not any apparent sigmoid increase in organic matter as in Linsley Pond.

The "resolution" (*i.e.*, the sharpness of the boundary) between lake types based on chironomids may be overstrained. This is particularly true of the distinction between *Chironomus anthracinus* and *C. plumosus* lakes, but even the "mesotrophic" *Stictochironomus* and *Sergentia* lakes are hard to delimit, as Brundin (1949) has emphasized. Such lakes need more thorough investigation of their chironomid populations.

The initial dominance of *Sergentia coracina* in Myers Lake, and its eventual extirpation, are believed to indicate a moderately severe hypolimnetic oxygen depletion initially, which increased gradually and steadily to the present severe oxygen depletion. It is believed that the reduction in the volume of the hypolimnion was the main cause of this gradual and steady increase in oxygen deficit.

The reasons for the fluctuations in the productivity of *Sergentia* are not known. Estimates of the rate of sedimentation (through pollen analysis and radiocarbon dating) may give insight into the reasons for variations in chironomid productivity. This would constitute a valuable complement to the information gained from comparative limnology.

Although a better technique than sieving will probably have to be devised before valid estimates of the true abundance of *Chaoborus* populations can be made, it is probable that the present methods are adequate to gain a rough idea of the relative changes in abundance of this organism during the developmental history of the lakes.

This investigation has shown that by the application of available knowledge on morphology and ecology more can be done toward the accurate identification of chironomid and *Chaoborus* remains than has been appreciated heretofore. Such accurate identification has only begun to be exploited in terms of lake typology and zoogeography.

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The Sensory Basis for Homing in the Longear Sunfish, *Lepomis megalotis megalotis* (Rafinesque)¹

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ABSTRACT

The ability of the longear sunfish to return to a home range from an unfamiliar area 200 to 350 feet away was studied in Richland Creek, Indiana. Home range is defined as the area over which an animal normally travels, and return to a home range is called homing.

It was assumed that homing has a sensory basis. Attention was focused on the olfactory and visual senses, since these senses are known to be involved in homing in other species of fishes. Experiments were conducted with four major categories of fish: (1) blinded fish, (2) fish with olfaction impaired, (3) fish with both vision and olfaction impaired, and (4) controls. An electrical shocker was used for the collection of all fish.

The homing abilities of the three categories of treated fish were compared with the homing ability of controls. Blinded individuals homed as quickly and accurately as controls. For example, a total of 114 longear sunfish with the lenses removed from their eyes were displaced. Forty-one of these were recaptured, and 31 (76 per cent) homed. Of 109 controls displaced in the same manner, 35 were recaptured. Twenty-seven of the 35 (77 per cent) homed. There is no significant difference between the homing abilities of the control and lens removal groups.

Fish whose olfactory mechanism was impaired moved at random. They could not return to the home range with the precision shown by controls. A total of 136 longear sunfish with their olfactory epithelium cauterized was displaced. Thirty-one were recaptured; 17 (55 per cent) returned to their home ranges, while 14 (45 per cent) remained in the area to which they were displaced. Of 112 controls, 32 were recaptured. Twenty-nine of the 32 (91 per cent) homed. A test of independence of the homing abilities of these two groups indicates a significant difference (chi-square = 8.38 with 1 d.f., $p = <0.005$).

Those individuals with both senses impaired were entirely disoriented. Only one fish out of the 40 displaced was recaptured. This specimen was taken a considerable distance downstream from the release point.

Indirect evidence was derived from a study of the relative homing abilities of control longear sunfish moving upstream toward home versus those moving downstream toward home. The precision of those fish homing in the upstream direction was found to be greater than that of those moving downstream. This is to be expected since odors from the home range would be carried to fish homing in the upstream direction by the current.

The main conclusion was that the olfactory mechanism of the longear sunfish mediates homing. The fish search for their home range and apparently recognize the area by a characteristic odor, or possibly a combination of odors.

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INTRODUCTION

The longear sunfish (*Lepomis megalotis*) is one of the most common sunfishes in the smaller streams and lakes of mid-western United States. In streams it is found almost exclusively in pools, and only an occasional individual is collected in riffles. The population studied contained few fish larger than five and one-half inches total length. Insects, crustaceans, and small fishes constitute the major food items in its diet. The spawning season of the longear sunfish of Richland Creek, Indiana, probably centers in May, but ripe fish have been taken during June, July, and early August. Like the other sunfishes, the longear sunfish is a nest-builder.

The purpose of this study is to formulate a theory, based on sensory-physiological evidence, that will explain the ability of the longear sunfish (Fig. 1) to return to a home range when displaced experimentally. Home

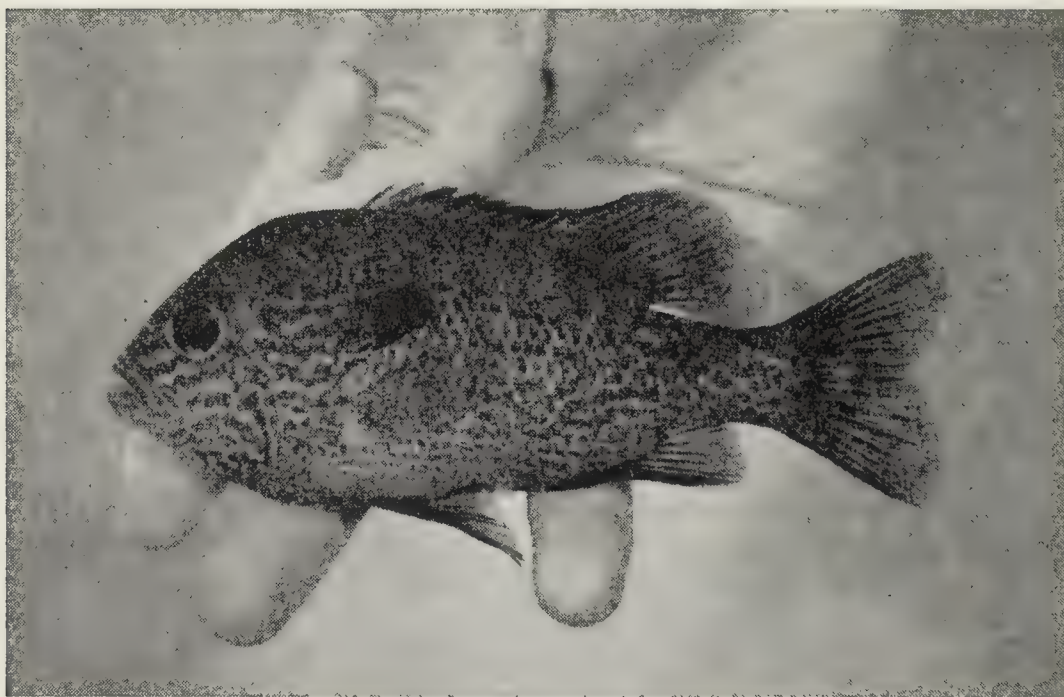


FIG. 1. Longear sunfish photographed in life. This individual is a male measuring five and one-half inches total length.

range is defined as the area over which an animal normally travels (Hayne 1949). Attention is focused on the olfactory and visual senses, since they are known to play leading roles in orientation of other species of fishes. Before the results of the sensory experiments conducted in the field are considered, evidence will be given to show that the home range concept is valid for the longear sunfish.

The behavioral phenomenon known as homing has been defined in a variety of ways throughout the literature. Allee *et al.* (1950) stated that homing reactions are concerned with an animal's becoming so adjusted to a specific area that returns are made, perhaps to the precise spot, when activities or environmental accidents cause removal. Williams (1957) defined homing as follows: "Homing is taken to mean a periodic return of a certain animal to a certain area that is small compared to the total home range." Homing can also be used in anadromous fishes

to describe the return of spawning adults to the stream of their nativity, or parent stream. Gerking (1959) reviewed homing in fishes and cited examples that conform to each of the above definitions. He stated, "... apparently no single mechanism or motivation will explain homing," and thus proposed a general definition: "Homing refers to the choice that a fish makes between returning to a place formerly occupied instead of other equally probable places." This general definition is adopted here.

The various modes of homing orientation have been classified by Griffin (1952). Hasler *et al.* (1958) have modified Griffin's classification, and their modification is given here:

- Type I: The ability of an animal to find home by relying on local landmarks within familiar territory and the use of exploration in unfamiliar areas.
- Type II: The ability to maintain a constant compass direction in unfamiliar territory.
- Type III: The ability to head for home from unknown territory by true navigation. This involves a "sextant" type of mechanism.

Homing of the longear sunfish will be classified with respect to the above types.

Gerking (1959) discussed the fact that 21 fish species are known to return to the general area from which they came after having been displaced by natural migratory habits, by accident, or for experimental purposes. These include six freshwater stream fishes, nine freshwater lake or pond species, and six ocean forms in addition to the well-known anadromous and catadromous forms such as the eel, shad, and several species of salmonids. The list includes 10 families representing four orders. Homing is thus widespread in a taxonomic sense, and is exhibited by fishes living in very diverse environments.

Only a few studies have been made on the homing behavior of members of the Centrarchidae, the family to which the longear sunfish belongs. Larimore (1952) studied the homing ability of the smallmouth bass (*Micropterus dolomieu*) in Jordan Creek, Illinois. Twenty-three bass were displaced distances of 0.1 to 0.8 mile upstream or downstream from their home pools. Of 31 transfers, 17 returned to their home pool one to two weeks after displacement. Some of the fish were transferred more than once. A significant number of the bass thus moved toward home accurately and in a relatively short time.

Larimore also displaced 50 longear sunfish during his experiments. Only nine of the longear sunfish returned home. He realized that his data on this species were not conclusive, but he suggested that the longear sunfish has a lower capacity for finding its way back to a home pool than the smallmouth bass. The following year, however, Gerking (1953) reported a single experiment that demonstrated that longear sunfish will return to a home pool in significant numbers when they are displaced a shorter distance. A sample of longear sunfish from a downstream pool was transported across a long riffle a distance of approximately 350 feet to an upstream pool. A majority of the sample crossed the riffle and moved downstream to the home pool. Twenty-six of 35 recaptures from the sample transported upstream returned to the home pool within two

weeks after displacement. Gerking first interpreted this movement as a "result of competition between 'foreign' and well-established individuals." Later, however, (Gerking 1957) the movement was interpreted as true homing behavior. My own results extend these initial observations on the longear sunfish considerably, and show that the species is able to return to its home range quickly and accurately after having been displaced 200 feet or more.

Other studies have dealt with the homing of centrarchids in lakes and ponds. Shoemaker (1952) demonstrated that pumpkinseeds (*Lepomis gibbosus*) in Lake Myosotis, New York, would return to home areas when displaced to other areas of the lake experimentally. Of 72 pumpkinseed recaptures, 62 (86 per cent) were taken at the home area while 10 (14 per cent) strayed. Similar observations have been made for the pumpkinseed, largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), and rock bass (*Ambloplites rupestris*) of Sugarloaf Lake, Michigan, by Cooper (1953); however, in this experiment the fish had only to distinguish the "home-half" of the lake from the "opposite half." Rodeheffer (1941, 1945) has suggested that a homing response is exhibited by the rock bass of Douglas Lake, Michigan.

Parker (1956) studied the homing behavior of the largemouth bass, bluegill, pumpkinseed, and bluegill x pumpkinseed hybrid populations of some northern Wisconsin lakes. The fish were caught in fyke nets placed at eight stations around the periphery of the lakes, marked as to area of initial capture, and displaced to a central point in the lake. In Dadek Lake for example, 84 of 216 largemouth bass returned to the home area. This represents a return of 38.9 per cent, but making an allowance for those fish that would return at random the resulting homing percentage was 25 per cent. Parker suggested the possible existence of two groups in the population, one that homes and one that moves at random. A somewhat different concept, that of a sedentary and a mobile group, was proposed by Funk (1957) for stream fishes.

Hasler and Wisby (1958) studied the return of displaced largemouth bass and green sunfish (*Lepomis cyanellus*) in ponds and lakes in Wisconsin. Individual green sunfish in a shallow pond appeared to return in the spring to the same area occupied the previous summer. The return of individual fish to their nests was also studied by attaching a pencil-shaped bobber to them with a nylon thread about three feet long and a hook. The authors showed by direct observation that the return path of these fish after release is direct and does not include movements that could be described as wandering or random in nature. Displaced largemouth bass did not return to their capture-area with the precision shown by the green sunfish.

The present work is divided into three parts: (1) demonstration of the home range concept, (2) demonstration of the homing ability of the longear sunfish, and (3) the reporting of experiments designed to test the role of vision and the sense of smell in the homing response. The same basic assumption is made in this paper with respect to homing that has been made elsewhere (*e.g.*, Collins 1953, Hasler 1956a), namely that homing must have a physiological basis and cannot be explained by speculation concerning extrasensory perception. The first two parts con-

firm the work of other investigators and form a framework for the experimental work which follows. The major contribution is that olfaction is more important in explaining the homing ability of the longear sunfish than is vision. This implies that the water of each pool or riffle, or even a part of either, has a characteristic smell that the fish can recognize.

SENSORY PERCEPTION AND FISH ORIENTATION

Vision and its relation to orientation

A number of types of orientation in fishes depend upon vision; the possible role of this sense in the homing of the longear sunfish was analyzed. These types are: (1) maintenance of position by moving in relation to a field of visual stimulation, (2) formation and maintenance of fish schools and aggregations, (3) orientation in tide pools based on learned topographical features of an area, and (4) sun-orientation in fishes allowing return to a home area.

Lyon (1904) placed killifish (Cyprinodontidae) into a long bottle filled with water and corked it to eliminate the effect of current. When the bottle was moved in one direction along the algae-covered wall of a large tank, the fish promptly swam to the opposite end. They were not oriented by a current but by "apparent motion" of the wall of the tank. Similarly, when the experimenter permitted this bottle to float in the current of a small tide stream, the fish quickly swam to the upstream end. In another test minnows swam in the direction in which a substratum of transverse black and white stripes was moved beneath the glass bottom of their aquarium. Several species of fishes tested by Lyon showed this ability to move in relation to a field of visual stimulation.

A number of workers have studied the role played by vision in the formation and maintenance of fish schools and aggregations. The subject is extensively reviewed by Morrow (1948); only one example is given here. Keenleyside (1955) studied the reaction of a single rudd (Cyprinidae: *Scardinius erythrophthalmus*) to a school of the same species in an aquarium and found that the test fish did not react to the group of rudd while blinded with aluminum-foil caps, but reacted strongly to them when able to see. While blinded the test fish swam back and forth from end to end of the aquarium showing no reaction to the other fish enclosed in a glass jar within the aquarium. After removal of the blinds it swam directly to the jar containing fish and seldom left it during a 30-minute test. It followed closely the movements of the other fish, sometimes trying to get into the jar with them, and sometimes staying motionless beside the jar.

Aronson (1951) studied orientation and jumping behavior in the goby (*Bathygobius soporator*). Direct observation and simple transfer experiments showed that ordinarily these fish are so well-oriented before jumping that they always land safely in a neighboring pool or in the open water. Under usual conditions the fish could not possibly see neighboring pools before leaping. Various possible factors in this orientation were tested. Aronson suggested that in swimming over the tide pools at high tide, the gobies learn the general topographical features of a limited area around the home pool, a basis for orientation when locked in the pools at low tide.

Hasler and co-workers at the University of Wisconsin have investigated the possibility of fishes using sun-orientation to find their ways back to home areas, a phenomenon well known in insects. Hasler (1956b) investigated the influence of environmental reference points on learned orientation in a minnow (*Phoxinus laevis*). Fish were trained to find food at the "north" position in a circular tank. The starting cue was the burning of a light 45° from north. When the tank was rotated 180°, the fish sought food in the south position. Elimination tests proved the reference points to be minute marks on the wall and floor of the tank, and not the artificial "sun." Hasler suggested that the unusual ability of the fish to thus appraise his immediate environment, and to use inconspicuous landmarks for orientation, aids in explaining the homing ability of lake and shore fishes.

Hasler *et al.* (1958) studied sun-orientation in the white bass (*Roccus chrysops*) of Lake Mendota, Wisconsin. White bass were displaced from two spawning grounds on the north shore of Lake Mendota to mid-lake, a distance of 2.4 kilometers. From a sample of 1,366 fish, 181 were recaptured in fyke nets and less than nine per cent erred by being recaptured at the net on the adjoining spawning ground. Fish to which floats were attached for direct tracing moved generally north from the center of the lake when released on clear days. Fish released between the two spawning grounds also moved north on clear days. On cloudy days, however, or if blinded with plastic eye caps, they moved at random. After these and other experiments were conducted, the authors suggested that the white bass possesses a sun-compass mechanism which is used for orientation in open water. The fish are able to maintain a constant compass direction at any time of day by using the sun as a point of reference. Upon reaching the vicinity of shore, however, they appear to locate their specific home areas by other methods. Sun-orientation is also discussed by Braemer and Hasler (1958).

Olfaction and its relation to orientation

Olfaction is known to play an important role in the orientation of fishes, since some find their food by the sense of smell. The role of olfaction in the homing response of the longear sunfish was analyzed, because the studies summarized below pointed to the possibility that it might be involved in the homing of this species.

A number of workers have shown that the sense of smell is very acute. Walker and Hasler (1949) studied the ability of the bluntnose minnow (*Pimephales notatus*) to detect and discriminate between odors of a number of aquatic plants. For example, the bluntnose minnow could discriminate between the odors of *Myriophyllum exalbescens* and *Ceratophyllum demersum* in training experiments. Hasler and Wisby (1950) found that the same species was able to detect the presence of a pure chemical, phenol, in concentrations far below the threshold for man.

Brett and MacKinnon (1954) investigated the sense of smell in migrating adult coho (*Oncorhynchus kisutch*) and spring salmon (*O. tshawytscha*) by pouring dilute solutions of each of 54 substances into the path of salmon moving up a fish ladder. Dilute water rinses of mammalian skins were found to have distinct repellent action. The

chemical properties of this repellent have been investigated (Alderdice *et al.* 1954, Idler *et al.* 1956). L-Serine, a component of human hand rinses, was found to elicit a typical alarm reaction in salmon, but the effects were neither so dramatic nor of such long duration as the response obtained by the unaltered hand rinse (Idler *op. cit.*).

Craigie (1926) studied homing behavior in sockeye salmon (*O. nerka*) of Deep Water Bay, British Columbia, by severing the olfactory nerves. He suggested that olfaction was involved in the migration of these fish to the Fraser River, but his results were of limited value since the home stream was not positively known, and insufficient recaptures were obtained to arrive at a definite conclusion.

Hasler and Wisby (1951) postulated that river and creek waters contain some characteristic odor to which young salmon become conditioned while in the stream, and to which they orient upon reaching the parent stream as mature migrants. Their theory embodies the principle that a salmon returning to its parent stream reacts differently to the odor of that stream than to any other. In order for a salmon to return to its home stream there must be the possibility of a differential reaction, not a simple response to a repellent or an attractant. This guiding odor must remain constant from year to year and have meaning only for those salmon that were conditioned to it during their early freshwater life. Salmon fry, *O. kisutch*, could discriminate between the odors of two Wisconsin creeks, as could the bluntnose minnow.

A field experiment was conducted to test the effect of olfactory occlusion on migrating silver salmon (Wisby and Hasler 1954). Fish were captured in traps in Issaquah Creek, Washington, and its east fork. The olfactory pits of approximately one-half the fish were occluded before all were displaced to the Issaquah River about one mile below the juncture of the two streams. The control salmon showed an excellent ability to repeat their original choice at the stream juncture; the treated fish did not show this ability. The latter were not able to differentiate between the two streams and distributed randomly. The results were in accord with the assumption that the fish were relying on their sense of smell in making this choice. The possibility that vision could assist in this orientation is not ruled out, however, since all of the salmon had normal vision.

Attempts to arrive at an explanation of the role played by smell in the homing of non-anadromous stream fishes have thus far failed to be conclusive. Miller (1954) put forth the hypothesis that cutthroat trout are guided by smell in finding home, because in his experiments the trout that were displaced downstream from their home areas were more successful in returning to the home areas than those displaced upstream from them. Before we can accept this hypothesis without reservation, data must be presented on trout that have had their olfactory mechanism impaired, and the role of sight must be investigated.

Dence (1956) discussed the migration behavior of a dwarf sucker (*Catostomus commersonnii utawana*) with an injured brain. Both of the olfactory nerves, as well as all of the left and part of the right olfactory lobes, were missing in this specimen. The fish failed to leave the North Inlet of Wolf Lake, New York, and return to the lake following

spawning as did the other suckers. This fact was said to substantiate the theory of Hasler and Wisby (1951) that olfactory stimuli may be factors in the homing of migrating fishes. The negative response of a single specimen is not in my opinion sufficient evidence on which to base judgments of the sensory mechanism responsible for homing. The injury may have altered behavior in many respects.

Stuart (1957), who performed an excellent study of the homing movement of brown trout (*Salmo trutta*) from lochs to spawning streams in the vicinity of Pitlochry, Scotland, attempted to apply the technique of Wisby and Hasler (1954). A sample of 113 trout was transported from one tributary stream across a reservoir to a second tributary stream. The olfactory pits of 58 were plugged; 55 were released without treatment as controls. A total of 30 fish made the return journey across the reservoir; 17 of these were untreated controls. Nine trout crossed the breadth of the reservoir with the olfactory plugs in position. No positive conclusion could be drawn due to the small number of recaptures and the fact that further evidence is required regarding the effectiveness of this method of olfactory occlusion. Also, one would have to rule out the possibility that vision, particularly sun-orientation, is involved in this homing ability.

Other senses involved in orientation

It is difficult to assess the roles of taste, hearing, the semicircular canals, the kinesthetic sense, and the lateral line sense in orientation, particularly as related to homing. This is due to a lack of experimental evidence on these subjects. Only the lateral line organs, which detect water currents, are discussed here.

In an aquatic environment where visual orientation is of reduced accuracy, the lateral line organs are said to be capable of supplementing vision by helping to localize objects at a distance. These objects may either be moving, and thus constitute the focal point of a mechanical disturbance, or their presence and localization may be perceived and accurately computed from the time relations of reflected water waves set up by the swimming movements of the fish itself (Lowenstein 1957). Lowenstein stated: ". . . the latter case would fundamentally conform with the principle of 'echo-location.' A fairly accurate three-dimensional sensory representation of the topographic features of the immediate environment, as well as the localization of moving objects in the vicinity, may thus be assumed to be mediated by this sense organ in the absence of visual orientation either in darkness or in a turbid medium." The role of this localization of objects in homing, if any, is not known.

DESCRIPTION OF THE CREEK AND STUDY AREAS

The field experiments were conducted on Richland Creek, a bedrock stream in Greene County, Indiana. The stream meanders through limestone country where it has cut through the topsoil to the underlying bedrock. The water is always murky. Secchi disc readings vary from two inches after a rain to two and one-half feet when the creek is clearest (Gerking 1950). The creek is fed by springs. Some flow of water is generally maintained. The width of the stream in the areas studied ranged from 10 to 35 feet.

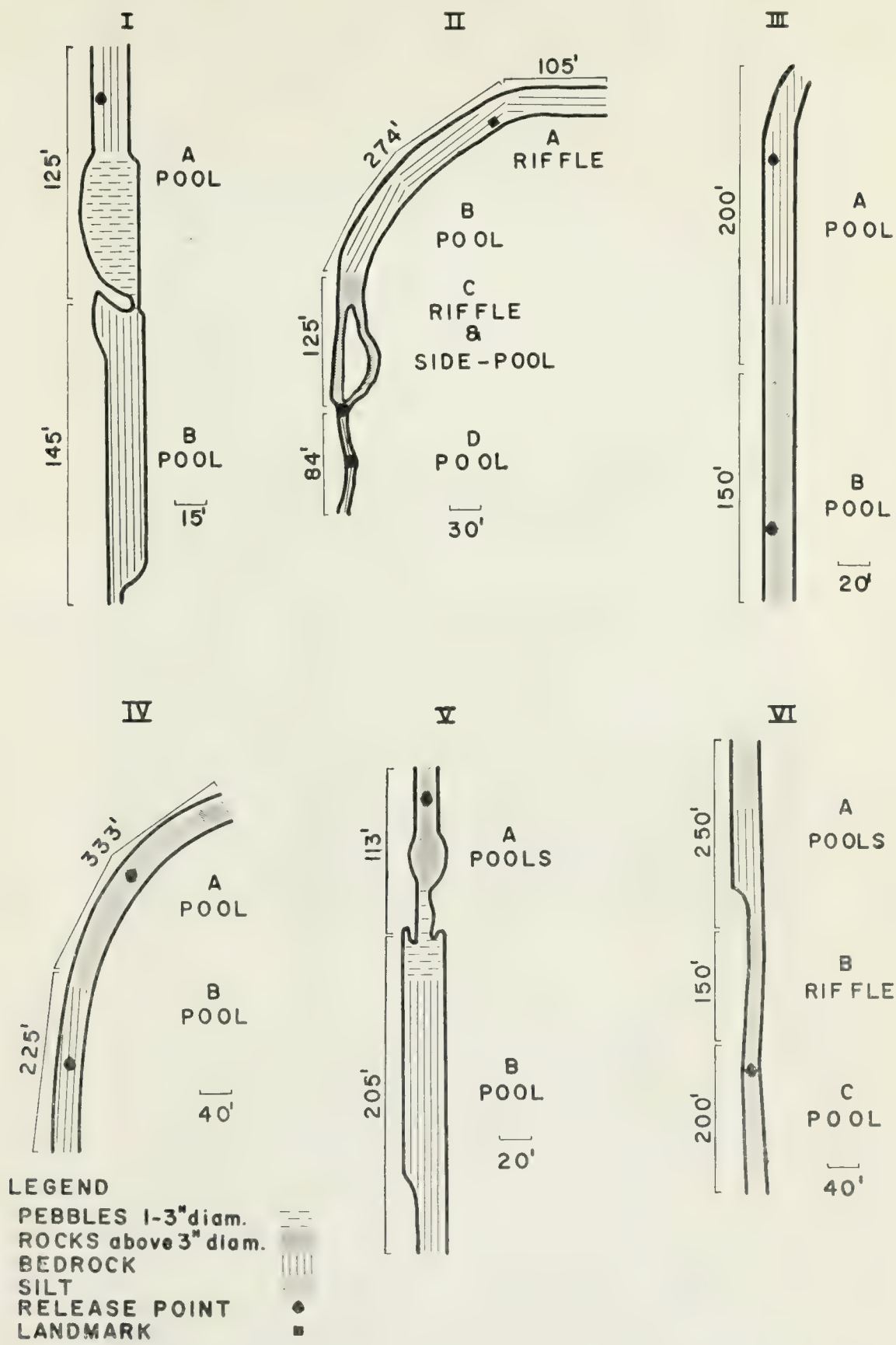


FIG. 2. Diagrams of the six study areas. The stream flows from A to B.

Six study areas were utilized. Since the various areas differed with respect to length, depth, type of bottom material, and pool or riffle composition, they are described briefly here and diagramed in Figure 2. All depths given are approximate average depths.

Study Area I: The upstream portion of Study Area I (section A) consisted of a pool 125 feet long with a depth of three feet. The downstream portion consisted of a pool 145 feet long with a depth of one and one-half feet (section B). A chute three feet long, three feet wide, and six inches deep connected the two sections. The study area is bounded on both ends by additional pools.

Study Area II: This study area consisted of four sections designated A, B C, and D, respectively, beginning upstream. This method of designation of the various sections of a given study area is used throughout this paper. Section A is a riffle 105 feet long and 10 inches deep. Section B is a pool 274 feet long and two feet deep (Fig. 3). Section C is a riffle



FIG. 3. Section B of Study Area II. The stream flows in the direction of the foreground. It is 30 feet wide at this point.

125 feet long and six inches deep with a sidepool, caused by dichotomy of the stream, approximately 75 feet long and two feet deep (Fig. 4). Section D is a pool 84 feet long and one and one-half feet deep.

Study Area III: This study area consists of a continuous pool 350 feet long and two and one-half feet deep. The pool was arbitrarily divided into an upstream section A (200 feet long), and a downstream section B (150 feet long). The boundary between these two sections is, of course, an artificial one, and was chosen because a landmark was present at that point.

Study Area IV: A continuous pool 558 feet long with a depth of three feet makes up this study area. The pool was arbitrarily divided into two sections, 333 and 225 feet long, respectively.

Study Area V: Upstream section A consists of two pools totaling 113 feet in length, separated by short riffles (10 to 20 feet long) from



FIG. 4. Section C of Study Area II facing downstream. The large piece of driftwood in the center of the picture was deposited there by receding waters following heavy rains. The side-pool to the right is 10 feet wide.

downstream section B, which consists of a pool 205 feet long. The various parts of section A vary in depth from 18 inches to two feet; section B is two and one-half feet deep.

Study Area VI: Two pools and a connecting riffle make up this area. Upstream section A consists of a series of interconnected pools totaling 250 feet in length and 18 inches deep. The riffle (section B) is 150 feet long and two feet deep. Only a 200-foot segment of the lower pool was utilized for section C. The downstream boundary is, therefore, artificial.

METHODS

Laboratory Investigations

A. Vision

Laboratory experiments were done in order to devise or test methods of blinding that would be suitable for field experiments. The methods were employed in the field experiments in the same fashion as in the laboratory, if laboratory experiments indicated their feasibility. Four different methods of blinding fishes experimentally were used with varying degrees of success: (1) chemical cautery using phemerol, (2) surgical removal of the eyes, (3) blinding with plastic eye caps, and (4) removal of the lenses from the eyes.

A three per cent aqueous solution of phemerol (benzethonium chloride) was used for blinding, following the method of Hasler and Wisby (1950) for minnows. The solution was injected into the posterior chamber of the eyes of longear sunfish until it oozed out around the needle. A one milliliter syringe equipped with a No. 24 needle, or smaller, was used. This method was discontinued because the injection altered the behavior of the fish. Several individuals swam around in circles very rapidly, and

"turned cartwheels" at the same time. Such behavior often resulted in collisions with the sides of the tanks. The behavior began 24 to 32 hours following injection, and the fish died 10 to 20 hours later. In other instances the fish died without behaving in such a dramatic way. The time lapse between injection and death was usually two to three days, but in a few cases death occurred a few minutes after the injection. Control fish injected with distilled water were not affected. Apparently phemerol has different effects on different species.

Surgical removal of the eyes, following section of the optic nerve, was attempted in the laboratory under heavy urethane anesthesia. Although heavy mortality resulted, a field experiment was carried out using this method.

Sperry and Clark (1949) used blinders made of tantalum foil in order to blind the goby (*Bathygobius*) for laboratory experiments. The blinders were inserted between the eyeball and the free external cornea through an incision in the skin dorsal to the cornea just large enough to permit passage of the cap. This type of blinder did not impair eye movements, but its use in the field would be difficult due to the time necessary for its placement on the fish. Keenleyside (1955) used a blinding method which consisted of placing a small circular piece of aluminum foil over each eye. The edges of the foil cap were pushed in under the rim of the eye socket, and when the cap was made slightly larger in circumference than the socket it caused no irritation.

Hasler *et al.* (1958) used a plastic eye cap which fits under the rim of the eye socket. I adopted their technique. Dies (Fig. 5) were made

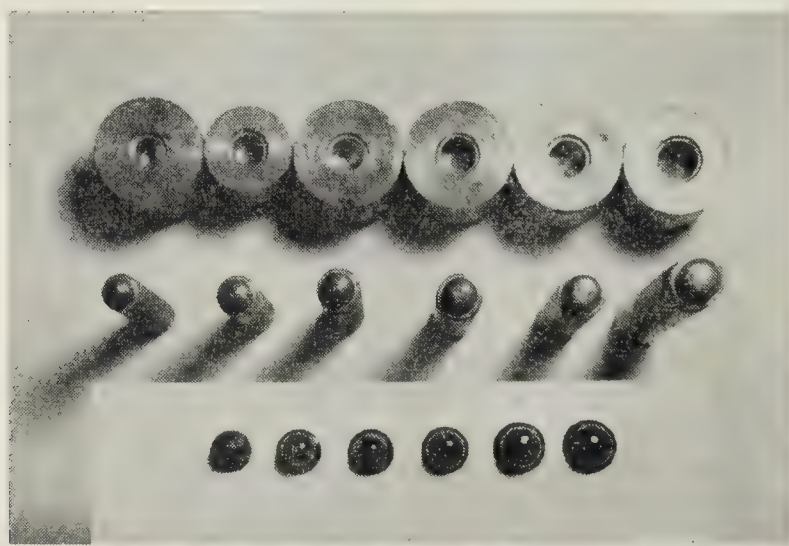


FIG. 5. Dies used to stamp out the plastic eye caps, and a sample of the six sizes of caps made for the longear sunfish.

by a machinist, and the caps were formed from preheated, 0.01-inch thick plastic on a drill press. Each die consisted of a male and female part. Eye caps were made with outside diameters of 8.5 to 11.0 millimeters, at intervals of one-half millimeter. The depths of the caps varied from five to six millimeters. The lip which fits under the edge of the eye socket must be critically measured. The caps for longear sunfish require a lip approxi-

mately one millimeter wide. The caps made by the writer were painted with black enamel. They were fitted onto the test fish under water. No anesthetic was used.

Disadvantages of the eye caps are: (1) at least 25 per cent of the eye caps are lost in field experiments over a period of five days, (2) installation yielding a tight fit often results in injury to the animal, (3) installation requires excessive handling of the fish, and (4) fungus growths develop under the caps.

The lens can be removed from a longear sunfish eye quickly and with little difficulty. A slit was made in the cornea from top to bottom with a pair of sharp-pointed scissors, and the lens popped to the surface when the center of the eye was pressed with a pair of forceps. The operation was first done under urethane anesthesia, but it was later found that this precaution was unnecessary. Mortality following the lens removal operation is negligible. The entire operation requires approximately 30 seconds per individual.

To test the vision of treated specimens, experiments were performed to determine if longear sunfish without their lenses could sight-feed, which is their characteristic method of acquiring food. A ringstand supporting a test tube containing four mealworm larvae (*Tenebrio*) was placed in front of several 15-gallon tanks, each containing one fish. The test tubes were placed in the same position at the center and oriented so that they were one-eighth inch from the glass of the tanks. For a period of 15 minutes a particular individual was observed, and the number of times it struck at the mealworms in the test tube was recorded. When sufficient data were obtained on each fish with the lenses intact, the lenses were removed and the experiments were repeated.

B. Olfaction

The olfactory mechanism of the longear sunfish was studied grossly and microscopically in the laboratory in order to see what methods of impairing the mechanism might be suggested by its anatomy. Three methods were studied: (1) cutting the olfactory nerve, (2) heat cautery of the olfactory rosette, and (3) latex occlusion of the olfactory pits.

The olfactory nerve of the longear sunfish lies so deep that a considerable amount of tissue must be removed to facilitate cutting it. This method was abandoned in favor of the other two.

Heat cautery was done by heating a blunt needle one millimeter in diameter and 25 millimeters long in the flame of an alcohol lamp until red hot. The needle was immediately inserted into the anterior naris of the fish and manipulated until the olfactory rosette had been seared. This operation was carried out under urethane anesthesia. Examination of fish treated in the laboratory showed that the method destroys most of the rosette.

Occlusion of the olfactory pits of the longear sunfish was feasible because they are blind sacs that are not connected with the mouth cavity. The occlusion method consists of filling each pit with liquid latex from a five milliliter veterinary syringe. A cotton ball saturated with a weak acetic acid solution (two parts glacial acetic acid in 98 parts water) is then pressed against each naris in order to harden the latex.

The olfactory mechanism of fish injected with liquid latex was studied under a dissecting microscope. If injected properly the latex will fill not only the primary nasal sac, but also the two accessory pouches on each side which open from the posterior part of the primary sac. The accessory pouches act as water pumps during the protractile and retractile movements of the upper jaw (Eaton 1956). The latex thus serves to decrease, and possibly block completely, the current of water coursing through the olfactory pits. Only one in 20 of the olfactory pits injected in the laboratory was incompletely blocked by the latex plug.

Field experiments

A. General design of the experiments

Home range experiments: The first type of field experiment was conducted in order to corroborate the home range concept for the longear sunfish. A sample of fish was removed from a segment of stream, marked with a fin-clip, and replaced in the same segment. At one- and two-week intervals the area was sampled to learn how many of the fish remained in the area. Adjacent areas upstream and downstream were also sampled in order to search for stray fish. Year-to-year recaptures were also obtained between the years of 1956 and 1958.

Homing experiments: The majority of the experiments were designed to learn whether or not the longear sunfish would return to its home range after being displaced 200 feet or more. Fish were removed from a segment of stream and transported either upstream or downstream from this area. The assumption was made that they were transported outside of their home areas, since Gerking (1953) found that the size of the home range of the longear sunfish was no greater than 100 to 200 feet. Three groups of fish were used in these experiments: (1) control or untreated individuals, (2) specimens with the olfactory mechanism impaired, and (3) fish with impaired vision. The relative abilities of these different groups to return to the home range were studied. All were fin-clipped for future identification.

The longear sunfish used in these experiments were two to six inches long (total length). Specimens smaller than two inches are not sampled adequately. They were not measured individually because this would have increased the time required for handling.

B. Blinding methods

Application of eye caps, surgical removal of the eyes, and lens removal were all carried out in the field in the same manner as in the laboratory. Eye caps could be fitted onto only the larger fish, because smaller caps could not be manipulated quickly.

C. Olfactory occlusion and heat cautery

Both of these methods were carried out in the field in the same manner as in the laboratory. The fish seemed to suffer no ill effects from either method following their release in the field.

D. Sampling methods

During the summer of 1956 when the study was initiated, collections were made with a 115-volt, direct current generator which proved inadequate. It was replaced in turn by alternating current generators supplying 150 to 230 volts, respectively. In addition to a portable generator the shocker unit consisted of about 200 feet of electrical cable and a pair of hand electrodes. The collecting team consisted of two men wearing plastic waders. One member of the team, wearing rubber gloves, manipulated the electrodes; the second member netted the stunned fish and placed them into a pail which he carried. Only longear sunfish were netted. Periodically the fishes in the pail were placed into a live box located nearby.

Collecting was always begun at the downstream end of the study area. After entering the stream the team proceeded along the nearest bank for a distance of approximately 15 feet. After this portion was shocked the team turned toward the center of the stream and proceeded in the opposite direction until the starting point was reached. This procedure was repeated again and again until the 15 linear-foot segment of stream was sampled. The team then moved upstream and continued sampling in the same manner until the entire study area was covered. The entire area was sometimes sampled again if returns were low. The second and subsequent samplings produced few fish. Nevertheless, the samples provided only one-fourth to one-half of the total population on any given day as determined from experiments in which control fish were released. A considerable number of fish were able to avoid capture by swimming around the collectors beyond range of the electrical field.

In some instances the boundaries between sections of pools were in open water. When the experiments were begun, blocking nets were used to prevent any fish within one area from swimming into an adjacent one. The blocking nets consisted of two straight, one-quarter inch mesh seines 50 feet long and six feet deep. Fish were never concentrated near the blocking nets, therefore the nets were not used later in the study.

RESULTS

Laboratory investigations

A. Vision

Effect of lens removal on sight-feeding: Normal longear sunfish (lenses intact) struck at the mealworms an average of 16 times per 15-minute period in the experimental apparatus previously described. The lenses were removed from the same animals, and the experiment was repeated on three successive dates. The treated individuals failed to strike a single time. In order to demonstrate that the above fish were not affected by the operation on the eye in such manner that they would refuse to strike at the bait because of shock or some other factor, an experiment was also conducted using two longear sunfish that were blinded on August 3, 1956. The latter had been in the laboratory for over 14 months, and presumably their recovery was complete. No strikes

were made by these two fish in a total of 12 trials involving a time period of three hours.

The blinded individuals frequently passed within one-quarter inch of the mealworm larvae, but the fish failed to see the larvae. Normal longear sunfish on the other hand dart at the worms immediately after the worms are placed into the test tubes.

The above experiments prove conclusively that lens removal results in a loss of the ability to sight-feed. However, longear sunfish with their lenses removed are probably able to perceive light, because the retina is still intact following the operation. It is not known whether or not this ability to perceive light would be of any value to the fish. Data from eye cap and eye removal experiments indicate that it could play at most a small and insignificant role in homing.

Changes in behavior following lens removal: Certain changes in behavior occur following the removal of the lenses from the eyes of longear sunfish: (1) fish occasionally swim backwards for a few days following the operation, (2) fish with their lenses removed often list to one side, (3) they develop sedentary habits and become more cautious of the presence of other fish in the laboratory tanks, and (4) a marked thigmotactic response is shown by adherence to the bottom and sides of the tanks.

B. Olfaction

The longear sunfish is a sight-feeder, and its feeding behavior is not altered by heat cautery of the olfactory epithelium, or following occlusion of the olfactory sacs with liquid latex. Fish so treated will feed shortly after treatment. No other behavioral differences were noted.

Field experiments

A. Control experiments corroborating the home range concept

Short-term experiment: On July 17, 1956, a sample of 34 longear sunfish was captured from section B of Study Area II, marked, and released in the middle of the same section. The great majority of recaptures taken on later dates were in section B (Table 1). Only two fish

TABLE 1. Movements of 34 control longear sunfish following capture on July 17, 1956, marking, and return to the stream area from which they were removed.

Date	No. fish recaptured	No. of home fish	No. of stray fish
7/23/56	16	14	2
7/30/56	15*	15	0

* Since all recaptures taken on July 23 were returned to the section from which they were captured, they were available for subsequent recapture on July 30, 1956. All recaptures are released for subsequent recapture at a later date unless otherwise stated in the experiments which follow.

strayed, and both were found in section A, upstream. The recapture rate was high in both samples, 44 and 47 per cent, and it is doubtful that many fish strayed beyond the boundaries of the study area. Adjacent areas were sampled downstream for a period of three summers, but no strays from this experiment were found.

Long-term experiment: Sixty-six fish were marked in Study Area III during 1956 and 1957, and sampled in 1958 in order to study the extent to which longear sunfish remain in the same pool from year to year. All individuals were removed from section A. The history of ten longear sunfish that remained in their home area from year to year is given in Table 2. Only two (not included in Table 2) strayed into section B;

TABLE 2. Year-to-year occupancy of section A, Study Area III, by ten longear sunfish.*

No. of fish	Originally marked in August 1956	Subsequent Dates Collected in III-A		
		July 1957	July 1958	August 1958
2	Marked LP	--	--	Recaptured
2	--	Marked RV	Recaptured	--
2	--	Marked RV	--	Recaptured
1	Marked LP	Recaptured & marked RV	Recaptured	--
1	Marked LP	Recaptured & marked RV	--	Recaptured
1	--	Marked RV Recaptured & marked LV	Recaptured	--
1	--	Marked LV	--	Recaptured

* LP signifies removal of the left pectoral fin. RP designates right pectoral, RV right ventral, and LV left ventral.

these were marked in August, 1956, and were recaptured during August, 1958. Adjacent areas of stream both upstream and downstream were sampled on numerous occasions, but no other strays were found.

The results of both the short-term and long-term experiments agree with those of Gerking (1950, 1953), who established the concept of home range for the longear sunfish in another part of the same stream.

B. Homing experiments with vision impaired

Lens-removal experiments: Three displacement experiments were conducted with fish from which the eye lenses had been removed (Table 3, Experiments 1-3). Four, five, and 11 days, respectively, were allowed for their return. Different time periods elapsed between marking and recapture in the various displacement experiments conducted because of:

TABLE 3. Homing performance of longear sunfish with impaired vision following displacement upstream or downstream from their home ranges.

Exp. No.	Direction displaced	Displaced from	Displaced to	Dates	No. fish marked	No. fish recaptured	No. fish homing	No. fish not homing*	Distance traveled by fish homing**
<u>Lens Removal</u>									
1	Downstream	II-B	II-C	6/26/57	43	—	—	—	
				7/1/57	—	15	11	4	260
2	Upstream	I-B	I-A	8/7/56	40	—	—	—	
				8/11/56	—	20	14	6	175
3	Upstream	V-B	V-A	8/12/58	31	—	—	—	
				8/23/58	—	6	6	0	200
<u>Eye Caps</u>									
4	Downstream	II-C	II-D	8/18/58	11	—	—	—	
				8/21/58	—	6	4	2	100
5#	Downstream	III-A	III-B	8/18-23/58	23	—	—	—	
				8/21-25/58	—	6	4	2	200
6#	Upstream	III-B	III-A	8/22-23/58	13	—	—	—	
				8/23-25/58	—	5	4	1	200
<u>Eye Removal</u>									
7	Downstream	III-A	III-B	9/26/57	47	—	—	—	
				10/1/57	—	6	6	0	200

* Fish that remained in the area into which displaced.

** Distance from the release point to the middle of the section into which the fish homed expressed in feet.

Only five to seven large fish were collected in any one section. Therefore several small samples were displaced over a period of a few days.

(1) weather conditions which often prevented collecting, (2) availability of transportation facilities, and (3) availability of a field assistant.

In Experiment 1, 43 fish were collected from II-B (Study Area II, section B) and displaced to the release point on the boundary of II-C and II-D (Fig. 2). The fish that homed could return to II-B only if they took the route across the riffle of II-C, because there was a permanent barrier to movement at the upstream end of the side-pool. This barrier consisted of rocks and a dense growth of aquatic vegetation (Fig. 4). Nevertheless, 11 of 15 recaptures had returned to their home range five days following displacement (Table 3). Four fish with their lenses removed stayed in the side-pool. A similar experiment was done with controls (Experiment 10). The latter were released at the same release point; 10 of 12 recaptures were taken in their home range seven days following displacement (Table 4). The controls did not encounter the barrier mentioned above, because a rise in water level of the stream at the time this experiment was conducted enabled them to swim over it.

Experiment 2 is similar to 1, except that the fish were displaced upstream. Forty fish with their lenses removed were displaced from I-B to I-A. Twenty of these were recaptured four days following displacement; 14 had returned to their home range, while six remained in the area to which they were displaced (Table 3). Figure 2 shows the narrow chute between I-B and I-A that the fish had to find before they

TABLE 4. Homing performance of control longear sunfish following experimental displacement upstream or downstream from their home ranges.

Exp. No.	Direction displaced	Displaced from	Displaced to	Dates	No. fish marked	No. fish recaptured	No. fish homing	No. fish not homing	Distance traveled by fish homing
8	Downstream	III-A	III-B	8/6/56 8/20/56	66 —	— 19	— 19	— 0	200
9	Downstream	III-A	III-B	7/9/57 7/10/57	36 —	— 19	— 19	— 0	200
10	Downstream	II-B	II-C	8/11/58 8/18/58	37 —	— 12	— 10	— 2	260
11*	Downstream	VI-A	VI-C	8/20/58 8/27/58 9/5/58	43 — —	— 6 3	— 2 3	— 4 0	325
12**	Upstream	IV in part	Pool above IV	Summer 1951 2 weeks later	61 —	— 35	— 26	— 9	350
13	Upstream	IV-B	IV-A	7/30/57 7/31/57	46 —	— 13	— 10	— 3	265
14	Upstream	V-B	V-A	8/27/57 8/28/57 9/2/57 9/10/57	26 — — —	— 10 11 10	— 0 3 7	— 10 8 3	200

* The majority of the fish displaced were small (two to three inches total length). Also, the study area was extremely turbid.

** Conducted by Gerking (1953).

could return to their home range. Experiment 3 is not discussed in detail because it is similar to Experiment 2 and yielded comparable results.

For statistical analysis the results of Experiments 1, 2, and 3 (Table 3) were pooled and compared with the results of Experiments 10, 13, and 14 (Table 4). These particular control experiments were selected because the time intervals between release and recapture of the fish were comparable to the time intervals that elapsed in the lens removal experiments. A total of 114 fish with their lenses removed was displaced, and 41 of these were recaptured. Thirty-one of the 41 recaptures (76 per cent) returned to their home areas. The control experiments involved a total of 109 fish; 35 of these were recaptured. Twenty-seven of the 35 recaptures (77 per cent) returned to their home ranges. The similarity of the return of control and blinded groups is striking. A chi-square test of independence of the two groups shows that it is extremely unlikely that they represent separate populations (chi-square = 0.047 with 1 d.f., $p = 0.81$). It is concluded on the basis of these data that visual recognition of the environment is not necessary for homing to occur in the longear sunfish population studied.

Eye cap experiments: A total of 47 longear sunfish was fitted with eye caps. The details of displacement and the movements of these fish are summarized in Table 3. Two experiments in which 22 individuals were fitted with caps, but no recaptures were obtained, are not included.

The eye-cap data are limited, but there is an indication that specimens fitted with eye caps behaved abnormally. Three longear sunfish with eye

caps intact (not included in Table 3) strayed out of the study areas and were recaptured. Those with their lenses removed were never found outside the study areas. For example, none strayed out of Study Area I when Experiment 2 was conducted unless they moved several hundred yards away. A segment of stream 100 yards long upstream from I-A was sampled, in addition to a segment 50 yards long downstream from I-B. No strays were found in either segment. The high recapture rate for the lens removal experiment also indicates that the number of strays was minimal.

Essentially the same results were obtained in all of the eye cap experiments, so they were pooled. Experiments 4, 5, and 6 (Table 3) show that 12 of 17 eye-cap recaptures returned to their home ranges. Although the data are limited, it is concluded that vision is not necessary for homing to occur in the longear sunfish.

Eye removal experiment: A total of 47 longear sunfish was involved in this experiment. A low recapture rate resulted for the eye removal group, presumably due to high mortality following the operation. Six fish were recaptured in their home range five days after displacement; they had traveled an average distance of 200 feet from III-B to III-A (Table 3). The data are limited, but they give added support to the conclusions reached for the lens-removal and eye-cap experiments.

Behavior of an individual blinded fish: On July 10, 1958, a sample of 12 eye-capped longear sunfish was taken from II-B and displaced to the release point at the lower boundary of II-C. Rain fell on July 10 and 11, and by July 12, the water in the creek had risen almost three feet above its normal summer level.

On August 11, 1958, one of the individuals previously fitted with eye caps was taken in the uppermost part of II-B near a large rock which served as a distinctive landmark (Fig. 2). Both of the eye caps had been lost, but the fish was blinded due to a fungus growth. The eyes were sunken far back into their sockets, and a large amount of scar tissue was evident. Several other similar occurrences have been observed in the field and laboratory. The fish was lean and emaciated when taken on August 11, but was again displaced to II-C with a group of controls. It was marked again by fin-clip so that this individual fish could be recognized if it were recaptured at a later date. On August 16, 1958, the fish was taken again in II-B less than 10 feet from the spot where it was taken on August 11. The fish was then transported to II-C for the third time. It was recaptured on September 8, 1958, just three feet from the rock landmark in II-B (Fig. 2). The distance traveled by the fish on each of these three homing trips was approximately 350 feet.

This individual was brought to the laboratory on September 8, in order to determine whether or not it was blind. Sight-feeding tests like those performed with fish without lenses in their eyes were carried out. It was found that the fish could not sight-feed.

The eyes were dissected under a dissecting microscope. The lens was missing from each eye and the remaining tissues were atrophied. It was therefore concluded on the basis of behavioral experiments and examination of the eyes that the fish was blind.

The behavior of this individual is discussed in detail here because

it strongly suggests two important points with regard to homing in the longear sunfish: (1) homing can be accomplished without the aid of vision, and (2) homing movements are precise, that is, the fish returns to a precise part of the stream and not just to a particular pool.

C. Homing experiments with olfaction impaired

Heat cautery of the olfactory epithelium: Study Area IV was sampled on August 27, 1956. A total of 76 longear sunfish was taken from IV-A, and 60 were taken from IV-B. The olfactory rosette of the fish of both groups was cauterized. Following treatment and marking by fin-clip, a reciprocal displacement was made: fish taken from IV-A were displaced to the release point in IV-B, and those from IV-B were displaced to the release point in IV-A (Fig. 2).

Fifteen of the 76 fish displaced to IV-B were recaptured seven days after displacement. Nine of the 15 had returned to IV-A, while six remained in IV-B (Experiment 15a, Table 5). In the reciprocal experiment

TABLE 5. Homing performance of longear sunfish whose olfactory mechanism was impaired prior to their displacement upstream or downstream from their home ranges.

Exp. No.	Direction	Displaced from	Displaced to	Dates	No. fish marked	No. fish recaptured	No. fish homing	No. fish not homing	Distance traveled by fish homing
<u>Heat Cautery</u>									
15a	Downstream	IV-A	IV-B	8/27/56	76	—	—	—	
				9/3/56	—	15	9	6	265
15b	Upstream	IV-B	IV-A	8/27/56	60	—	—	—	
				9/3/56	—	16	8	8	265
<u>Latex Occlusion</u>									
16	Downstream	II-B	II-C	9/4/58	38	—	—	—	
				9/8/58	—	5	3	2	260
17	Upstream	IV-B	IV-A	8/13/58	40	—	—	—	
				8/14/58	—	8	2	6	265

in which the fish that homed were moving downstream toward home, eight fish homed to IV-B and eight fish remained in IV-A (Experiment 15b, Table 5). There were no barriers to movement in the study area.

A control experiment (13) was conducted at Study Area IV on July 30 and 31, 1957. Forty-six fish were displaced from IV-B to IV-A as in Experiment 15b. The entire study area was sampled one day after displacement of the group. A total of 13 fish was recaptured, and only three of these failed to home (Table 4). It is obvious upon comparison of the results from Experiments 13 and 15b that the treated fish were not able to return to their home ranges with the same precision as the controls, even though they had several days in which to return.

Results from Olfactory Experiments 15a and 15b were pooled and compared with the results of Control Experiments 8 and 13 in order to determine the effect of heat cautery of the olfactory mechanism on homing efficiency. Thirty-one of the 136 fish in the olfactory experiments

were recaptured. Seventeen (55 per cent) homed, while 14 (45 per cent) remained in the area to which they were displaced. Thirty-two recaptures were obtained from the 112 controls that were released. Twenty-nine (91 per cent) returned to their home areas, and three (9 per cent) stayed in the area to which they were transported. A chi-square test of independence of these data indicates that the difference between the heat cautery group and control group is significant (chi-square = 8.38 with 1 d.f., $p = <0.005$).

On the basis of Experiment 15, in which 17 fish homed and 14 remained in the area into which they were displaced, it is concluded that a random distribution of recaptures resulted from random movement following loss of the olfactory sense. The olfactory sense thus mediates the return of the fish that home.

Blocking the olfactory pits with liquid latex: Two displacement experiments (16 and 17, Table 5) were conducted in which a sample of fish with the olfactory mechanism plugged with latex was transported away from the home range. Since the number of recaptures in both experiments was small, the results of the two were pooled. Five fish returned to their home ranges, eight remained in the area into which they were transported, and five (not included in Table 5) strayed beyond the bounds of Study Areas II and IV. One fish was found upstream from IV-A and the remainder downstream from II-D. If fish whose olfactory sense is impaired move at random, then it is not surprising that strays are found outside the study areas. Unfortunately, a search for strays was not made when the heat cautery experiments were conducted.

The pooled results given above were compared with the pooled results of control experiments 10 and 13 in order to ascertain the effect of latex occlusion on homing ability. In the control experiments, of 83 longear sunfish transferred 25 were recaptured. Twenty out of 25 recaptures returned to their home areas. A chi-square test of independence indicates that there is a difference in the precision of the homing response of the two groups (chi-square = 5.79, with 1 d.f., $p = 0.018$). The five fish that strayed out of the study areas were not included in the calculations. If they had been included the chi-square value would have been even greater. It is further concluded that the fish whose olfactory mechanism was occluded with latex distributed themselves at random, and that the random distribution resulted from a loss of olfactory discrimination. The above data indicate that the olfactory sense mediates the return of fish that home.

D. Homing experiment with olfaction and vision impaired

On September 11, 1958, a sample of 40 longear sunfish whose lenses had been removed and olfactory pits occluded with latex was displaced from II-B to II-D. Four days later all of Study Area II, a segment of stream approximately 100 feet long separating Study Areas II and III, and section A of Study Area III were sampled. Only one treated fish was recovered. This individual was captured in III-A, approximately 300 feet downstream from the point of release in II-D. Since neither treatment employed inflicts a heavy mortality on test fish, it is assumed that

the fish traveled beyond the boundaries of the study areas. The ability of the fish to orient with respect to their home range was lost following the impairment of both smell and sight.

E. Indirect evidence that olfaction is involved in homing

The data from heat-cauterized and latex-occluded fish present direct evidence that the olfactory mechanism is involved in homing. If this is accepted, then fish that move upstream toward their home ranges should have an advantage over those moving downstream, since odoriferous substances would be carried downstream by the current. A study of the data from untreated fish should shed light on this point.

The results of Control Experiments 8, 9, and 10 were pooled and compared with the pooled results of Control Experiments 12, 13, and 14 (Table 4). In the former experiments the fish moved upstream toward home, while in the latter they moved downstream. There were no barriers to prevent movement of these fish at the time the various experiments were conducted.

Fifty of the 139 fish moving upstream were recaptured; 48 of these returned to their home ranges, while two failed to return. Fifty-eight of the 133 fish moving downstream were recaptured. Forty-three traveled back to their home ranges, but 15 remained in the area to which they were transferred. A chi-square test of independence indicates that there is a significant difference between the homing abilities of the two groups (chi-square = 8.47, with 1 d.f., $p = < 0.005$).

The above results are, therefore, in accord with what would be expected if the longear sunfish were relying on the sense of smell to return to the home area.

DISCUSSION

The stated purpose of this study was to formulate a theory, based on sensory-physiological evidence, that would explain the ability of the longear sunfish to return to a home range when displaced experimentally. Undoubtedly such returns are made when the fish happen to be displaced under natural conditions of the environment. A previous study has treated the stability of fish populations in streams (Gerking 1950). Nine species (including the longear sunfish) were marked prior to a long period of rainy weather, which resulted in a flash flood and high water conditions in general. After the flood waters subsided, collections were made of fish marked 32 to 45 days previously. It was found that 75 per cent of the total number of recaptured fish were in their original location. The assumption was made that the fish maintained their positions during the flood. Such an assumption is difficult to prove because collection of fish under flood conditions is extremely difficult, if not impossible.

It is of interest, for purposes of the present study, to consider the alternative conclusion, namely that the fish were swept downstream from the home range during the flood. If this were the case the fish could return to the home area during the time that elapsed between the flash flood and the date upon which collecting in the stream was resumed. It is assumed that such return would be mediated by the same sensory

mechanism that allows longear sunfish to return to the home range when displaced experimentally.

In connection with the latter assumption, the writer has observed fish being swept downstream across riffles on numerous occasions when the streams were flowing at a normal level. Also, a common observation is that fish leave stream beds when they overflow and can be found in abundance in adjacent fields or flood plains. It is quite probable that fish leave their home ranges to find suitable feeding sites or breeding places. In all of these examples the fish are subjected to a foreign environment and must rely on their sensory mechanisms for return to their home ranges.

The behavior of an individual blinded fish indicated that homing in the longear sunfish involves a return to the precise spot which it formerly occupied. Considering that this individual returned a distance of 350 feet to a precise spot on each of three trips, the return of the fish to a home range after leaving it for the reasons given above seems quite possible.

Data have been presented to show that the concept of home range is valid for the longear sunfish. Gerking (1950, 1953) has shown that the home range of the longear sunfish is no more than 100 to 200 feet of stream, and the single long-term experiment conducted by the writer corroborates this fact. Since the fish are able to remain within this area in significant numbers over a long period of time, it is highly probable that whatever sensory mechanism enables the fish to return to the home range when displaced from it also enables them to remain in it barring environmental accidents or intentional trips beyond its limits.

If fish displaced in the field retain the eye caps, or survive following the eye removal operation, there is no question that any movement after the operation is accomplished while the fish is blind. However, it is possible that new lenses might regenerate. This does not appear to be the case, since Morrill (1906) and Stone and Sapir (1940) have confirmed the absence of such regeneration in *Fundulus heteroclitus*. Rasquin (1949) reported no return of vision in *Astyanax mexicanus* after removal of the lenses, and also no evidence for regeneration of the lens in this species. In fact the optic nerves of *Astyanax* ultimately degenerated following the lens removal. The writer examined longear sunfish with the lens removed in both the field and laboratory up to a period of one year, and found no evidence of regeneration. This possibility is therefore discounted.

Professor A. D. Hasler of the University of Wisconsin has used our method of latex occlusion of the olfactory pits for the study of green sunfish in ponds (Hasler 1958, personal communication). Sight is involved in the ability of green sunfish to return to their nests when experimentally displaced. When the olfactory pits of the green sunfish are plugged using the latex method, the fish return to their nests as readily as before. The latex injection does not appear to alter the behavior of the fish. Homing by means of the olfactory mechanism is more adaptive in stream fishes than in pond fishes.

Information is not available at this time to assess the effects of heat cautery on the behavior of the test fish. Field and laboratory tests indi-

cate that mortality following heat cautery is negligible. Individuals treated in this manner will feed readily in the laboratory.

The results of Control Experiment 14, in which the fish were displaced upstream from their home range, indicate that homing in the longear sunfish is a searching phenomenon. Six days following displacement only three of 11 recaptures had gone back to the home range. Seven of 10 recaptures had returned to the home range two weeks following displacement (Table 4). There were no barriers to prevent homing at any time during the experiment. Distance was probably not the cause of the slow return, because the fish of Experiment 13 traveled farther, and in addition, had only one day to make the return trip. In the opinion of the writer, the possibility that the pool in the middle of the study area contained odors foreign to the fish and caused confusion when the fish attempted to home should be considered. The same would also apply to Control Experiment 11, although in this instance the number of recaptures is too small to be conclusive.

Floats were attached to untreated fish with a piece of nylon line and a fish hook in the manner of Hasler *et al.* (1958). This method was not successful for tracing the movements of a given fish back to the home range, because the fish tangled the line under stones, in overhanging willows, and so forth. Upon release the fish swam 10 to 40 feet before becoming tangled, and observation of these fish following displacement showed that there was no tendency for the fish to swim in the direction of their home ranges. Their movements following release could be described as searching movements.

If the classification of homing summarized in the introduction were adapted to include olfactory orientation, the homing of the longear sunfish would be classified as Type I—the ability of an animal to find home by relying on local landmarks (odor cues) within familiar territory and the use of exploration in unfamiliar areas. It is assumed that the return of the individual fish to the landmark on three different occasions was accomplished in this manner, although the experimental proof is lacking. It is difficult to determine what sensory mechanisms are involved in the ability to return to a precise spot, and the writer is not the first to encounter this difficulty. Hasler *et al.* (1958) in their study of sun-orientation in the white bass of Lake Mendota, Wisconsin, concluded that a sun-compass mechanism is used for orientation in open water. However, upon reaching the vicinity of shore, the white bass appear to locate their specific home areas by other methods.

The control experiments indicate that shallow riffles or pools between the home range and the stream section into which fish are displaced are not barriers to the movement of fish back to their home ranges. In Experiment 14 for example, the fish had to cross two short riffles and an intervening pool in their trip downstream. Seven of 10 recaptures (70 per cent) had returned to the home range two weeks following displacement. In Experiment 13, the fish were moving downstream toward their home range, but merely from one end of a continuous pool to the other with no riffles or an intervening pool to cross. Thirteen fish were recaptured one day following displacement, and 10 (77 per cent) of these had returned to their home range. Comparison of these experiments indi-

cates that intervening riffles or pools do not significantly affect the percentage of fish that eventually home over the distances studied. The time required for homing to take place is, however, increased (Table 4).

Direct evidence based on the homing ability of fish whose olfactory mechanism was impaired or occluded, and indirect evidence based on the relative homing abilities of control fish displaced upstream or downstream from their home ranges, indicate that the olfactory mechanism of the longear sunfish mediates their return to a home range when displaced experimentally. This implies that the home range has a characteristic odor, or combination of odors, to which the fish can orient when the home range is reached. Evidence is presented to show that blinded fish are able to return to the home range as quickly and accurately as controls. This is in line with what could be expected, since the turbidity of Richland Creek would likely prevent visual recognition of the home range when it is encountered.

The present study has gone one step beyond previous studies that have dealt with homing in fishes (*e.g.*, Craigie 1926, Wisby and Hasler 1954, Miller 1954, Stuart 1957) in that the fish were obliged to use their olfactory mechanism to find their ways back to the home range while they were blind. This fact not only strengthens the data from fish whose olfactory mechanism was impaired, but eliminates the possibility that vision is an accessory mechanism involved in the homing of the longear sunfish.

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The Two Creeks Interval in Indiana Pollen Diagrams¹

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ABSTRACT

The Two Creeks Interval in a pollen diagram from Myers Lake in north central Indiana is demonstrated by an almost complete elimination of *Picea* and *Abies*, a large representation of *Pinus*, and midway through the section by a marked development of *Betula*. Percentages of non-arboreal pollens are much lower than in the two limiting cold zones, which may have had a tundra vegetation or at least taiga. Some of these same elements of change in pollen composition occur in many of the previous pollen diagrams from Indiana and are probably homologous. The question whether or not *Quercus* (and *Ulmus*?) became temporarily established in the northern half of the state during Two Creeks time cannot be decided on the basis of the present data.

INTRODUCTION

The Two Creeks Interval has not hitherto been recognized with certainty in pollen diagrams from the northern half of Indiana. This warm interval would be expected, because Indiana was continuously free of ice after the retreat of the glacier from the Valparaiso and Wabash moraines in middle Cary time, roughly 14,000-15,000 years B.P.

In the many pollen analyses published by Potzger and his associates *Picea* and *Abies* generally continue dominant from their maximum in late-glacial time to the bottom of the sections. Generally there are low percentages of *Quercus* throughout much of this interval, and occasionally small percentages of other deciduous trees. In a number of instances there is a marked development of *Quercus* below the *Pinus* maximum in pollen Zone B or even below the earlier *Picea-Abies* peak. Deevey (1953) has reasoned that this *Quercus* peak in Tippecanoe Lake may well derive from Two Creeks time, because it is associated with a marked increase in the carbonate content of the sediments—a change that would be expected during a warm interval.

This is the only hint in the literature that the Two Creeks Interval may be represented in Indiana pollen diagrams by detectable changes in the pollen curves. The present diagram from Myers Lake however, shows a well developed cold-warmer-cold sequence, which is here equated with the retreat of Cary ice from the state and with the Two Creeks Interval. Moreover, in many of the pollen diagrams by Potzger and his associates these same changes tend to occur, indicating that the Two Creeks sequence was not missed in the pollen analysis but merely was not recognized. Martin (1958) was disturbed by the fact that Potzger (Zumberge and Potzger 1956) failed to find high percentages of non-arboreal pollen (NAP) in Hartford Bog in southern Michigan. This lack of treatment and analysis of the NAP by Potzger *et al.* is the one

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feature that prevents certain correlation between the late-glacial deciduous zones in their diagrams with the Two Creeks sequence in Myers Lake.

The present study was made to help J. B. Stahl interpret the time relationships in the midge and *Chaoborus* succession observed in Myers Lake. The pollen diagram is based on the same core reported on by Stahl (1959).

GENERAL RELATIONSHIPS

Myers Lake in Marshall County, Indiana, is located in the Maxinkuckee Moraine, dating possibly from early Cary time about 16,000 years B.P. The glacial history of this region is complicated, so that although the Maxinkuckee Moraine itself was free of ice, end moraines were being deposited in northern Indiana for at least the next 2,000 years (Wabash and Fort Wayne moraines to the east). The Valparaiso Moraine to the south of Lake Michigan is believed to be approximately 15,000 years old, and ice remained in the southern Lake Michigan region until approximately 13,000 years B.P. These age relationships of the various moraines are based on an unpublished summary of Indiana radiocarbon dates by W. J. Wayne of the Indiana Geological Survey.

During the Two Creeks Interstadial ending approximately 11,000 years B.P. the ice retreated into northern Michigan or beyond. The Valdres advance brought a lobe down the Lake Michigan basin to the approximate level of Milwaukee, or even somewhat further south (Zumberge and Potzger 1956). With the retreat of this lobe the Midwest was not subsequently covered by ice.

Thus the Myers Lake vicinity was affected for perhaps 3,000 years by ice masses within 80 miles or less of the site. Following a long retreat of the ice, the Valdres lobe subsequently advanced to perhaps within 100 miles of the site.

METHODS

The core from Myers Lake was collected in meter-long monoliths by means of a Livingstone piston sampler. Samples furnished by Stahl from this core (see Stahl 1959 for a complete description of the core) were first treated in 10% HCl in a boiling water bath until there was no longer any ebullition of CO₂. The samples were then centrifuged, washed in distilled water, and placed in 250-ml beakers with 10% KOH on a mechanical stirrer hotplate until the sediment was completely deflocculated (ca. 10 min.), after which they were centrifuged and washed with distilled water. This material was then mounted in glycerine jelly stained with gentian violet. Although the lowermost samples had a considerable content of clay, silt, and fine sand, no attempt was made to concentrate the pollen by differential flotation (Frey 1955) or by digestion with HF. In any restudy of this or similar material, either of these concentration techniques should be used on the lowermost levels.

The slides were examined systematically at a magnification of 96 diameters, and all pollens and spores encountered were tabulated until at least 150 tree pollens had been recognized. The actual numbers for the individual samples ranged from 153 to 193. No attempt was made to identify the various types of non-tree pollens beyond the general cate-

gories of grasses, composites, sedges, Caryophyllaceae, and Chenopodiaceae, except for *Artemisia*.

In the general pollen diagram (Fig. 1) all trees and shrubs are included in the pollen sum. Other plants are expressed as percentages of this sum at each level studied.

RESULTS

Included in the pollen diagram are most of the trees and shrubs identified, and the dominant herbaceous types. The following supplementary information will help to understand the complete picture and to relate the results to other pollen diagrams from Indiana.

Tsuga—2 doubtful grains at 25.65 and 25.95 m.

Tilia—1 grain each at 25.75 and 27.40 m; a more or less closed curve (1 or 2 grains per level) from 23.00 m to the surface, with no definite maximum.

Salix—quite generally distributed, but usually only 1 grain per sample, with a maximum of 3; not a closed curve.

Liriodendron—single grains at 18.55, 19.35, and 22.59 m.

Juniperus—only low percentages (maximum of 4%); 4 grains total at 25.55, 25.65, and 25.85 m; small group of occurrences at 23.85-24.35 m, and a slight maximum near the bottom of the post-glacial oak dominance.

Liquidambar—single grains at 17.55, 19.35, 21.05, and 22.05 m.

Corylus—small numbers (1-4 grains per level) throughout, although not a continuous curve.

Ericales—1 grain at 23.95 m.

Non-arboreal pollens (NAP) are 10% or greater (maximum 20.2% at 24.55 m) at 19.95-20.05, 22.39, 23.55-24.55, 26.55, and 27.40-27.60 m. Even including the unknowns (some of which are undoubtedly spores instead of pollens) the percentages are 40% or less in the intervals 23.55-24.55, 26.55, and 27.40-27.60 m. These are the highest NAP percentages.

Aquatic plants are represented by single grains (*Myriophyllum* at 24.75 m, *Nymphaea* at 19.95 m), scattered grains (*Typha*: single grains at 19.05, 19.85, 23.10, 23.45, and 26.35 m), or a cluster of small percentages for *Potamogeton* from 24.95 to 25.85 m, with isolated occurrences at 19.75, 23.10, and 24.35 m.

Lycopods and polypods are generally, although not continuously, distributed in small percentages, with more nearly continuous distribution below 23.65 m.

The object called *Equisetum* occurred at all levels, sometimes in greater abundance than the arboreal pollens. This was a large grain which compared favorably with the *Equisetum* reference material. The two layers of the wall were distinct and separate, indicating that this grain is not *Larix*. No grains of *Larix* were positively identified.

The pollen diagram is readily separated into two parts by the sharp *Picea* peak at 23.65 m—the portion above representing post-glacial time, and the portion below including the 23.65-m level late-glacial time.

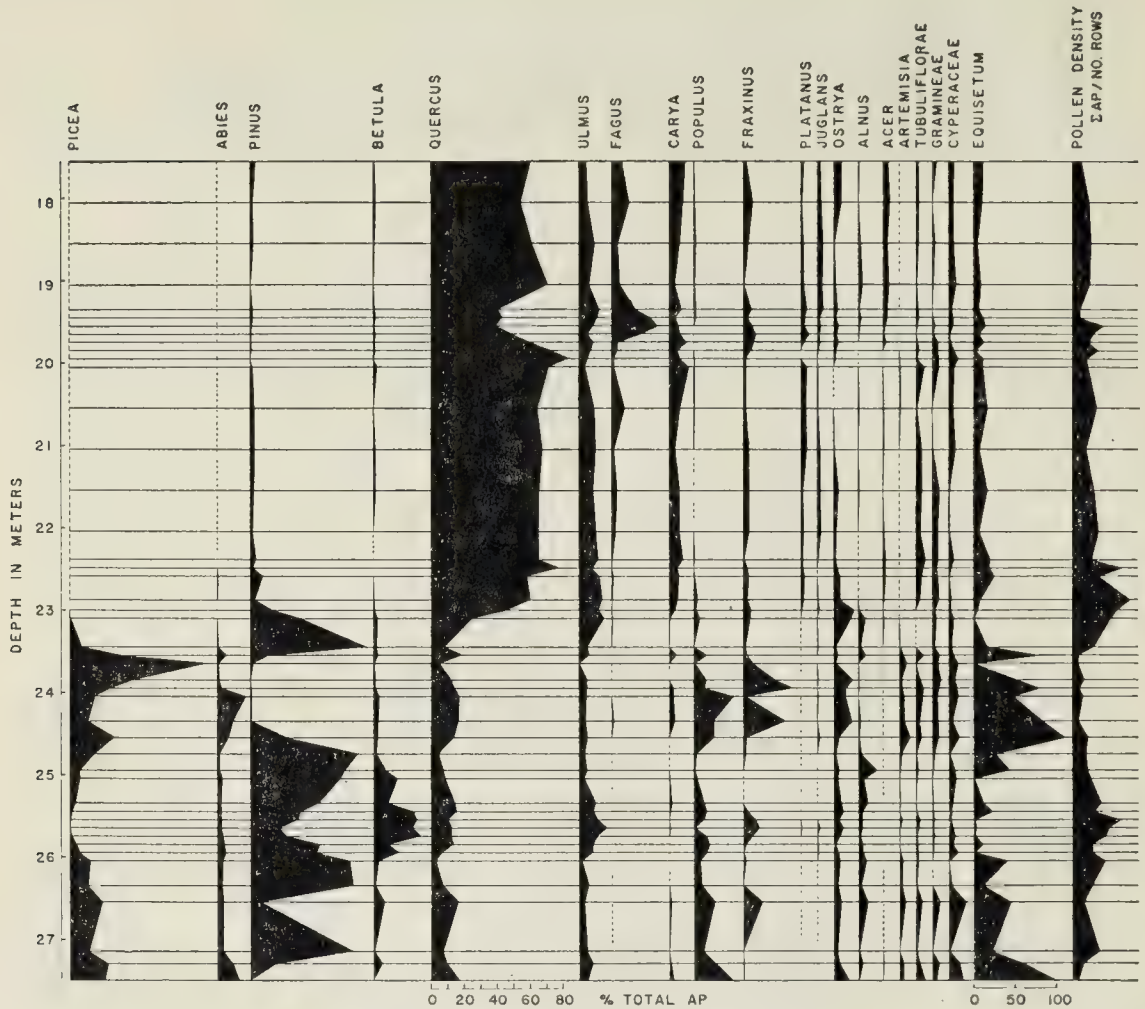


FIG. 1. General pollen diagram for Myers Lake. Included are all the important arboreal and herbaceous types.

Post-glacial time

Following the decline of *Picea* there is a sharp *Pinus* peak, constituting Zone B in Deevey's (1949) chronology. The *Quercus-Ulmus* phase to about 20.50 m is Zone C1. The *Quercus-Carya* maximum at 19.95 m is in Zone C2, as is the *Fagus* maximum from 19.35-19.65 m. From 19.05 m to the top of the sediments is Zone C3. This is a fairly typical sequence for the central Midwest, of gradual warming to a maximum in C2 time, with a dry period corresponding to the *Carya* peak, followed by cooling and a moister climate.

Late-glacial time

The late-glacial section in the Myers Lake core is more heterogeneous than any reported on by Potzger and his associates from the state. *Picea* and *Abies* are not continuously dominant, but rather are supplanted by *Pinus* during a considerable portion of this section. Between 25 and 26 m there is an almost complete elimination of *Picea*, and a complete

elimination of *Abies* at 25.45 and 25.55 m (Fig. 1 is incorrect in this respect), and the dominance of *Pinus* is interrupted by a great development of *Betula*. The percentage of non-arboreal pollen between 25 and 26 m is markedly less than at either higher or lower levels, amounting to only 3-7% of the total AP (or less than 15%, including the unknowns). Stahl (1959) also shows an increased carbonate content at this general level. All these changes indicate a marked climatic amelioration, which I would equate with the retreat of ice from Indiana in late-Cary time and extending through the Two Creeks Interval. The subsequent regression of *Pinus* and the rise of *Picea*, *Abies*, and *Populus* along with large NAP percentages seem logically correlated with the Valders readvance.

Below the Two Creeks section there are obviously marked changes in pollen composition that are not well defined in the present diagram because of the few levels analyzed. It seems likely that the pollen spectrum shown at 27.25 m is not in its correct depositional sequence. Except for the *Pinus* peak at this level, which may not be correct, there are gradual increases in *Picea*, *Abies*, *Populus*, and NAP percentages, the latter not so high as in the Valders section. All these changes indicate a cooler and more extreme climate than in the Two Creeks section of the core. It seems likely that the earliest sediments of Myers Lake are not represented.

The substantial percentages of warmth-loving deciduous trees in the late-glacial section in association with boreal forest components present a problem. Andersen (1954) faced with the same problem in analyzing a late-glacial pollen diagram from southern Michigan decided to regard the pollen of *Quercus*, *Carya*, *Fagus*, *Acer*, *Juglans*, *Ulmus*, *Fraxinus*, *Ostrya-Carpinus*, *Celtis*, *Liquidambar*, and *Vitis* as secondarily derived from interglacial deposits. Lacking actual pollen analyses of the tills of the region, Andersen's logical justification for this action is the present-day distinctness of the boreal and deciduous forests and their different environmental requirements.

For the same reasons and with the same likelihood of truth (which seems considerable) one can argue that these deciduous types in the late-glacial portion of the Myers Lake core are also predominantly rebedded. Recalculating the pollen composition of the section from 23.55 to 27.60 m on the assumption that only *Picea*, *Abies*, *Pinus*, *Betula*, *Populus*, and *Alnus* of all the tree types identified actually occurred in the region during this interval yields the late-glacial diagram shown in Figure 2. *Salix* should also be included, but it has been left out because of its very small percentages and irregular occurrence. The pollen curves in this diagram are similar to those in Figure 1 except that the various maxima are increased, and the minima are less extreme.

The curves for NAP and Unknowns show a marked minimum between 24.75 and 26.35 m, corresponding to the period of *Pinus* dominance and *Picea-Abies* regression. Midway through this interval is the pronounced development of *Betula*. *Populus* (*tremuloides*?) peaks bracket the *Betula* development in association with *Picea* and *Abies*. References to Figure 1 shows that the *Equisetum*-like grain also occurs in large percentages during the pre- and post-Two Creeks sections. All these features clearly emphasize the cold-warmer-cold climatic sequence of this section.

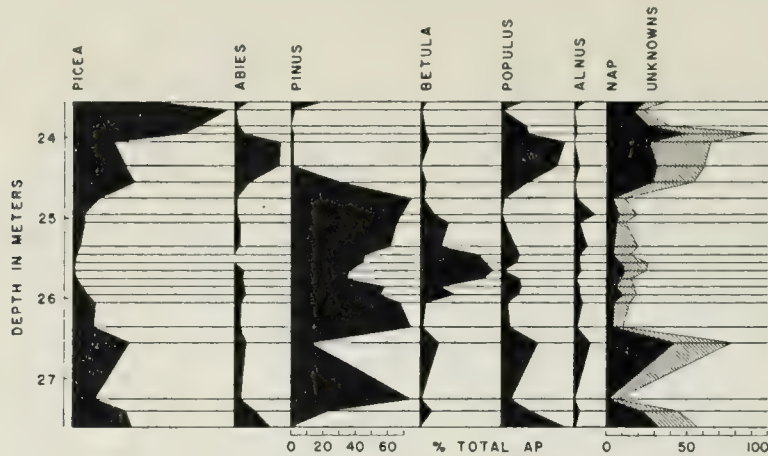


FIG. 2. Modified late-glacial pollen diagram from Myers Lake, based on the assumption that *Picea*, *Abies*, *Pinus*, *Betula*, *Populus*, *Alnus*, and *Salix* were the only trees actually established in the region and contributing to the pollen rain. NAP comprises grasses, composites, sedges, Caryophyllaceae, Chenopodiaceae, and *Artemisia*.

DISCUSSION

Although the Two Creeks Interval has not previously been recognized in pollen diagrams from Indiana, a study of the published diagrams shows that many of them contain elements of the same changes present in the Myers Lake diagram. The most obvious feature is a *Quercus* peak in late-glacial time, associated with distinct developments of *Betula* and/or *Salix*. This broadleaf complex sometimes is bracketed by *Picea*-*Abies* peaks and sometimes by *Pinus* peaks, the lower one of which may be quite weak. None of the other diagrams shows a late-glacial development of *Pinus* comparable to that at Myers Lake.

The diagram most strikingly similar to that of Myers Lake is Shoe Lake in Kosciusko Co., about 30 miles to the east of Myers Lake (Oliver 1950). Here *Abies* and *Picea* largely disappear in the middle late-glacial period and are replaced by *Pinus*, which midway in its dominance declines in favor of *Betula*, along with *Quercus* and *Ulmus*. Unfortunately, as is true of all pollen diagrams by Potzger and his associates, no mention is made of non-arboreal pollen. By analogy to Myers Lake, however, the Shoe Lake sequence must certainly derive from the Two Creeks warm interval. Regrettably, Oliver was more concerned with the high percentages of *Quercus* in late-glacial time than with the other changes in the pollen curves.

Reed Bog (Griffin 1950) in Randolph Co. in the east central part of Indiana also agrees quite closely with the late-glacial sequence in Myers Lake. In this diagram there are two pronounced peaks of *Picea* which bracket two lesser peaks of *Pinus* within late-glacial time. Between the two *Pinus* peaks is a marked development of *Quercus* associated with a *Salix* peak. Some *Ulmus* and small percentages of other deciduous trees also occur.

Jeff Bog (Keller 1943) in Wells Co. to the north of Randolph Co. shows two *Pinus* peaks, the upper one of which appears to be Zone B, between which is a *Quercus* peak possibly associated with *Salix*.

Otterbein Bog (Richards 1938) in Warren Co. in the west central part of Indiana has a suggestion of two *Pinus* peaks, bracketing a small *Quercus* development along with small percentages of *Alnus*, *Betula*, and *Salix*.

Yountsville Bog (Swickard 1941) in Montgomery Co. in the west central part of the state has a suggestion of a weak upper *Picea-Abies* development, with a marked *Betula* peak separating this from the lower and major *Picea-Abies* dominance.

In Mill Creek Bog (Swickard 1941) in Laporte Co. in the northeast part of Indiana a *Quercus* development in late-glacial time is associated with a marked *Salix* development. Here the lower *Pinus* peak although present is weak.

Round Lake Bog (Hamp 1940) in Starke Co. not far from Myers Lake has a small *Quercus* peak within the *Picea-Abies* period, but without any boreal deciduous trees associated.

Cranberry Pond (Barnett 1937) in Madison Co. in central Indiana shows a pronounced late-glacial *Quercus* peak associated with peaks of *Salix-Populus* and *Betula*-group. The upper coniferous peak is weakly developed.

Fox Prairie Bog (Prettyman 1937) in Hamilton Co. in central Indiana shows a pronounced late-glacial notch in the *Picea* and *Abies* curves, associated with a very pronounced peak of *Salix* and a lesser peak of *Betula*. *Pinus* is not shown as extending below this *Salix-Betula* interval, and *Quercus* had been increasing steadily from the preceding *Picea-Abies* dominance.

Bacon Swamp (Otto 1938) in Indianapolis, which is the southernmost major bog in the state and probably originated about 20,000 years B.P., shows a pronounced *Quercus*, *Populus-Salix*, *Betula*-group development between the *Picea-Abies* maximum and the *Pinus* peak in pollen Zone B. Above is a weak secondary *Picea-Abies* peak, and below is a weak *Pinus* peak.

Kokomo Bog (Howell 1938) in Howard Co. in central Indiana north of Indianapolis shows a *Betula-Salix-Quercus* development, which seems to occur during the declining phase of *Picea* and *Abies* but before the *Pinus* development in Zone B.

Examined in this light the *Quercus* peak in the diagram from Lake Tippecanoe (Patzger and Wilson 1941), which Deevey (1953) suggested derived from Two Creeks Time, takes on greater significance. It comes between two *Pinus* peaks, the lower one of which is weak, and it is associated with definite peaks of *Betula* and *Salix*. I agree with Deevey that this section of the diagram probably represents Two Creeks Time.

Other diagrams show either only a *Picea-Abies* period with no appreciable differentiation (Loon Lake in Kosciusko Co. and Altona Bog in Dekalb Co.—Moss 1940; Lakeville Bog in St. Joseph Co.—Hamp 1940; Culver Bog in Starke Co. and Shipshewana Bog in LaGrange Co.—Keller 1943; to name a few instances) or show *Quercus* continuing into the late-glacial sequence but not in association with peaks of any boreal deciduous trees (Pinhook Bog in Laporte Co. and Merrillville Bog in

Lake Co.—Guennel 1950). Pollen diagrams not showing any of these changes are possibly truncated at the bottom by incomplete sampling.

These changes in pollen composition which are regarded as originating in Two Creeks time are prominent in Myers Lake and Shoe Lake, and more subtle in the other pollen diagrams, although nearly always present. The coniferous pollen in a number of diagrams consists mainly of *Picea* and *Abies*, with lesser percentages of *Pinus*. A large representation of *Pinus*, in late-glacial time apparently was not regional for northern Indiana, but was controlled more by local conditions. Hence, any pronounced notch in the coniferous curves in late-glacial time may indicate the Two Creeks Interval.

Because of its abundance a maximum of *Quercus* within the late-glacial is often the most obvious indication of this warm interval, and sometimes *Quercus* is the only broadleaf indicator. Usually *Betula*, *Populus*, and/or *Salix* also increase at this time. Possibly Andersen's argument concerning rebedded pollen cannot be applied to northern Indiana. Possibly some *Quercus* (and *Ulmus*?) did become established here during Two Creeks time. This is logical to suppose, since the rate of deposition of silica and clay minerals (and hence of secondarily derived pollen) is generally reduced during warm intervals when there is a denser and more nearly complete cover of vegetation on the land. Pollen analysis of morainal material is needed to help decide this point, as well as radiocarbon dates from strategic levels. A more detailed study of the herbaceous pollens is also needed.

The substantial percentages of NAP bracketing the Two Creeks section in Myers Lake indicate at least taiga and possibly even tundra. All the diagrams from Indiana showing the Two Creeks pollen changes have almost complete dominance of *Picea* and *Abies* below this interval, suggesting that even at the latitude of Indianapolis where deglaciation occurred in the full glacial (more than 17,000 years ago), warmth-loving deciduous trees did not become established until Two Creeks time at the earliest, and possibly not until after the *Pinus* period (Zone B) in post-glacial time.

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